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COVER IMAGE

Discodoris boholiensis Bergh, 1877

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A Monographic Revision of Basal Discodorid Sea Slugs (Mollusca: Gastropoda: Nudibranchia: Doridina)

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TABLE OF CONTENTS

Abstract 3
Acknowledgments 4
Introduction 5
  Nomenclatural, taxonomic, and anatomical history of *Discodoris* 6
  Available species names 6
    Combinations 9
    Number of specimens traditionally used to describe new species 9
    Anatomical knowledge 10
    Diagnoses of *Discodoris* and phylogenetic relationships 10
Materials and Methods 12
  Establishing a list of species names 12
  Type material 13
  Additional material 14
  Material preparations 14
  Drawings and observations 14
  Plates 15
  Anatomical abbreviations 15
  Literature 16
  Species descriptions 16
  The use of the term 'species' and species delineation criteria 18
  Nomenclatural guidelines 19
    Form of species names 19
    Creation of new species names 20
    Nomenclatural status of species names and *nomina dubia* 20
    Designation of lectotypes and neotypes 20
  Cladistic analysis 20
    Taxon sampling 20
    Characters 21
    Parsimony analyses 23
Results 24
  Infra-specific character variation 24
    Color 24

        External morphology .25
        Digestive system .27
        Nervous system .29
        Reproductive system .30
Diversity and Synonymy . 33
    Cladistic analyses .34
        Topology and clade support .34
        Phylogenetic position of *nomina dubia* and poorly known species .35
        Metaphyly at the base of *Discodorididae* .37
        Classification .37
    Species binomials .38
        New combinations .38
        Problematic binomials .38
Discussion. 39
    Infra-specific character variation .39
    Estimation of species diversity .40
    Names of doubtful applications .41
    Lessons from history .42
    Biogeography .42
    Phylogenetic relationships within *Discodorididae* .43
    Future studies .43
        Species delineation and discovery .43
        Anatomical exploration .44
Species Descriptions. 44
    Discodoris 44
    Peltodoris 60
    Tayuva 77
    Sebadoris 127
    Asteronotus 174
    Rostanga 186
    Paradoris 199
    Geitodoris 202
    Aporodoris 207
    Platydoris 209
    Jorunna 214
    Hiatodoris 216
    "*Montereina*" 221
    Species that may or may not belong to Discodorididae 338
    Species that do not belong to Discodorididae 355
Comments on *Discodoris* and *Peltodoris* specimens mentioned in the literature without specific name (arranged by date) 358
References 362
Appendices 379

Basal discodorids, with an emphasis on *Discodoris* and *Peltodoris*, are revised for the first time. Hundreds of specimens were examined, including all types available. The individual variation of morphological characters is evaluated and taken into account for species delineation. Discodorid species are redescribed based on large numbers of individuals: e.g., 98 individuals were dissected for *Sebadoris fragilis* (Alder and Hancock, 1864). The nomenclatural status (valid name, synonym, *nomen dubium*) of 125 species names is addressed. Prior to the present study, there were 106 valid names, 13 synonyms, two *nomina dubia*, three permanently invalid names, and one *nomen nudum*; after revision, there are 39 valid names, 12 synonyms (out of the 13 former synonyms), 25 new synonyms, 27 *nomina dubia*, three permanently invalid names, one *nomen nudum*, and 18 names that refer to poorly-known species (which could be *nomina dubia*, synonyms, or valid names). Those numbers confirm again the critical need for taxonomic revisions in order to obtain a reliable knowledge on species biodiversity. Also, the high proportion of new synonyms and new *nomina dubia* is related to the fact that many discodorid species were described based on few specimens (of the 81 *Discodoris* species names, only five were originally created with more than four specimens). Another important factor that explains the high proportion of new synonyms and *nomina dubia* is the large number of incomplete original descriptions.

The supra-specific relationships of all species considered are addressed based on cladistic analyses. *Discodoris* is a clade including only two of all the former '*Discodoris*' species: *Discodoris boholiensis* Bergh, 1877, the type species of *Discodoris* under the *ICZN*, and *Discodoris cebuensis* Bergh, 1877. *Peltodoris* is a clade including only three species: *Peltodoris atromaculata* Bergh, 1880, the type species of *Peltodoris* under the *ICZN*, *Peltodoris mullineri* Millen and Bertsch, 2000, and *Peltodoris murrea* (Abraham, 1877). Also, several species are re-allocated to different discodorid clades: e.g., *Discodoris fragilis* (Alder and Hancock, 1864) transferred to *Sebadoris*, *Doris raripilosa* Abraham, 1877 to *Asteronotus*, and *Discodoris crawfordi* Burn, 1969 to *Rostanga*. However, 50 species (including 21 valid species, 17 *nomina dubia*, and 12 poorly known species) could not be placed in any of the discodorid clades (genera), and therefore are part of a metaphyletic group at the base of *Discodorididae*.

There are 50 species names for which we cannot use a generic name as the first part of the Linnaean binomial. This situation is handled in two ways. First, "*Montereina*," is used as a genus name for all the species that are part of the metaphyletic group at the base of *Discodorididae* (the quotation marks indicate that this genus name does not refer to a clade), which is compatible with the *ICZN* but contradicts phylogenetic principles. Second, the clade name *Discodorididae* is used as a clade address for all those species that cannot be placed in a clade of "generic" rank, which is compatible with the *International Code of Phylogenetic Nomenclature* (*ICPN*), or *PhyloCode*. The use of a supra-generic name instead of a generic name in front of a specific name is implemented in a monographic revision for the first time here, and represents a major change in our nomenclatural practices.

The vast majority of the species regarded as valid here are efficiently delineated based on morphological features (mainly the dorsal color, the shape of the radular teeth, and the reproductive system). However, in a few cases, such as in *Tayuva*, it seems that species cannot be distinguished morphologically. Future possible studies that could help solve those taxonomic issues are discussed. Seven new species are described. However, those new species are not formally named for a variety of reasons (mainly because not enough information was available). Finally, many new records are provided, especially from the tropical Indo-West Pacific.

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INTRODUCTION

Discodoris is one of the nearly 40 generic names of Discodorididae, along with *Geitodoris, Jorunna, Paradoris, Peltodoris, Platydoris, Thordisa*, etc. The monophyly of Discodorididae, confirmed here, is currently only supported by a series of morphological synapomorphies, such as a notched upper lip of the bilabiate anterior foot, and digitiform oral tentacles (Valdés 2002; Dayrat and Gosliner 2005).

At this stage, the species diversity of Discodorididae can hardly be estimated. Discodorididae, however, includes about 450 nominal species (available species binomials with a status that in many cases is undetermined). With 81 species names (plus five variety names and one subspecies names), *Discodoris* is by far the richest genus in Discodorididae. *Discodoris* species have been described worldwide, except in the Arctic and Antarctic; the majority is found in tropical waters; two species were described from deep-sea (West Pacific and Atlantic).

Before the present revision, the status of the vast majority of the species names was unknown. Only six species names were regarded as synonyms. Therefore, the first goal was to determine the status of all *Discodoris* species names, e.g., whether they should be regarded as valid names, synonyms, or *nomina dubia*.

Prior to this study, the supra-specific relationships among all those species were also largely unknown (Valdés 2002; Dayrat and Gosliner 2005). A few species names had been transferred from *Discodoris* into other genera, such as *Geitodoris* and *Paradoris* (Schrödl 2000; Dayrat 2006), but several major issues had never been addressed, such as whether *Discodoris* (or part of it) form a natural group, and the relationships among *Discodoris* species and species classified in *Discodoris*-like genera such as *Anisodoris* and *Peltodoris*. Addressing those questions was the second main goal of this revision.

The fact that a taxonomic revision of *Discodoris* was critically needed had been recognized for a long time. For instance, seventy years ago, Alice Pruvot-Fol (1934:68, translated here) pointed out that "there already [were] perhaps twice as many *Discodoris* species as there should be (if not three or four times)." This, interestingly, did not prevent her from creating a new species name in the same publication, *Discodoris vanikoro*, regarded here as a new synonym. Also, Thompson and Brown (1981:266) wrote: "There has been considerable confusion between the numerous species of *Discodoris* that have been proposed (often without adequate descriptions) and this is incapable of solution at present. There has also been an imperfect understanding of the precise limits of the genus *Discodoris* (as was discussed by Thompson 1973). *Discodoris* should probably be expanded so as to embrace *Diaulula* Bergh, 1880, *Peltodoris* Bergh, 1880 and *Anisodoris* Bergh, 1888 (which differ only in their lack of discrete oral armature)." Finally, Edmunds (1971:351) rightly wrote about the separation between *Discodoris* and *Peltodoris*, exclusively based on the presence *versus* absence of jaw plates on the labial cuticle, that it is a "very trivial character on which to separate two genera especially when we do not know how constant it is in a wide variety of specimens, nor whether it is absent in young animals and only developed as they mature." Many similar remarks are found in the *Discodoris* literature.

That nobody attempted to revise the group, even partially, is easily explained by too many species names to deal with, too many types to look for, too many specimens to borrow from too many institutions, too many non-type specimens to examine, too many publications to consider, too many incomplete anatomical descriptions published, too many other generic names to consider (especially *Peltodoris*, which includes 15 nominal species, by original or secondary combination, two of which are shared with *Discodoris*), etc.

Nomenclatural, Taxonomic, and Anatomical History of *Discodoris*

Available species names

Discodoris, a taxon traditionally ranked at the generic level, was named in 1877 by Bergh (Fig. 1) (1877a,b), for 11 species names, including four new combinations and seven new species names. Under the *International Code of Zoological Nomenclature* (1999, Article 69.1:72), the type species of *Discodoris* is *Discodoris boholiensis* Bergh, 1877, by subsequent designation by O'Donoghue (1926:2007). Bergh actually introduced the name *Discodoris* and several new species names (including the type species) in two publications published in the same year (Bergh 1877a, 1877b), of which the exact date of publication, however, is unknown. Because the species are only described in one of those publications (Bergh 1877a), Valdés (2002) recently selected Bergh's (1877a) contribution as the original description of the genus *Discodoris* (and its type species).

Selecting *boholiensis* as a type species was not the best solution because this species is quite distinct from the majority of *Discodoris* species. There exist today a total of 81 combinations with the generic name *Discodoris*. Although *Discodoris* was created in 1877, 16 *Discodoris* species names were created prior to 1877 with *Doris* as the first part of the binomial.

The history of *Discodoris* species names starts in 1804, when Cuvier described a new species

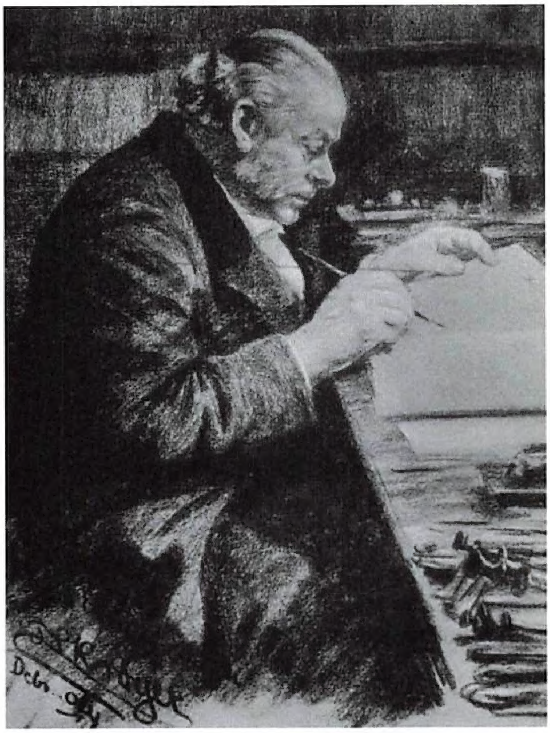

FIGURE 1. Portrait of Rudolph Bergh [1824-1909] (Vayssière 1910).

based on a specimen collected from the coast of Australia by Péron aboard *le Naturaliste* during the Baudin Expedition [1800-1804]. This new species, *Doris maculosa*, was described in a few lines, with no drawing. The type is lost (Alice Pruvot-Fol could not find it in the 1930s), and it is very difficult to determine which species Cuvier examined. Because Cuvier did not describe the shape of the oral tentacles, it is not possible to determine whether *Doris maculosa* is a discodorid or not. Pruvot-Fol (1935), however, rightly suggested that the specimen identified as *Doris maculosa* by Quoy and Gaimard (1832) was misidentified because the dorsal color described by Cuvier is different from the dorsal color described by Quoy and Gaimard: dark brown background with irregular blackish blotches (Cuvier's *maculosa*) *versus* white yellow background with black or brown rings (Quoy and Gaimard's *maculosa*). Based on a non-type specimen identified as "*Centrodoris maculosa* Cuvier" that she found in the MNHN collection, Pruvot-Fol (1935) created the new combination *Discodoris maculosa* and regarded (with a question mark) this name as a synonym of *Discodoris fragilis* and *Discodoris sordida*. According to Pruvot-Fol, this specimen was contemporary of Cuvier, who "very likely" ("très probablement") identified this specimen as *Doris maculosa* before someone changed the label. Even if Pruvot-Fol's hypothesis is correct, it still does not tell us what the type of *maculosa* was, and a synonymy between *maculosa*, *sordida*, and *fragilis* cannot be accepted with confidence. Here, *Doris maculosa* Cuvier, 1804, is regarded as a *nomen dubium*. Finally, Pruvot-Fol (1934) actually created a new species name, *Discodoris vanikoro*, for a specimen that she thought Quoy and Gaimard had misidentified as *Doris maculosa*. This specimen, which was re-examined for the present study, clearly is part of the same species as the type of *fragilis*.

The two next *Discodoris* species names were created in the 1830s. *Doris granulata* Ehrenberg, 1831, originally described from the Red Sea and transferred to *Discodoris* by Bergh (1877a), is regarded here as a *nomen dubium*. *Doris sordida* Quoy and Gaimard, 1832, is permanently invalid because it was preoccupied by *Doris sordida* Rüppell and Leuckart, 1828. It was replaced before 1961 by *Doris sordidata* Abraham, 1877, and re-allocated to *Discodoris* by Pruvot-Fol (1934). It is regarded here as a new synonym of *fragilis*.

The next period is dominated by two British naturalists from Newcastle-upon-Tyne, England: Alder and Hancock. The Hancock Museum, where Alder and Hancock's specimens are held, was named after Albany Alder and his brother John, naturalist as well. From 1846 to 1864, Alder and Hancock created six new species names of *Doris* which were transferred subsequently to *Discodoris*: two species from Great Britain, *Doris planata* and *Doris millegrana*, and four species from Madras, eastern India, based on the collection made by Sir Walter Elliot, including *Doris fragilis*, a common species in the tropical Indo-West Pacific and which has troubled taxonomists for decades. Four other *Doris* species names (subsequently re-allocated to *Discodoris*) were introduced by other naturalists during that same period. Gould named *Doris lilacina*, a common species in the Indo-West Pacific and several other regions in the world. Three Danish naturalists collaborated for *Doris crucis* Ørsted *in* Mörch, 1863. This species was first collected from two of the U. S. Virgin Islands (former Danish West Indies): from St. Thomas, by Riise, and St. Croix, by Ørsted. The latter also is the author of *crucis*, but the description was published by Mörch. In 1863, Cooper described *Doris sandiegensis* from the coast of southern California. Finally, Pease described *Doris nubilosa* in 1871, from Hawaii.

The next period, from the mid 1870s up to the beginning of the 20th century, could be called the Bergh period (Fig. 1), because it is largely dominated by Bergh's work. Rudolph Bergh, a Danish physician from Copenhagen, was one of the most prolific nudibranchers. Between 1875 and 1905, Bergh named 21 new species of *Discodoris* (by original combination), and created five species names that were subsequently re-allocated to *Discodoris*, such as *Peltodoris atromaculata* Bergh, 1880 and *Peltodoris mauritiana* Bergh, 1889. Although Bergh undoubtedly was the master during this period, two authors created other species names. Abraham (1877) named four new species of *Doris* subsequently transferred to *Discodoris*. Rochebrune described *Peltodoris sauvagei* in 1881, based on one specimen collected from the Cape Verde Islands by de Cessac, and transferred to *Discodoris* by Ortea et al. (1998).

The next period, which slightly overlaps with the previous one, saw the activities of four famous malacologists. Vayssière named three species of *Discodoris* in 1902, 1912, and 1919. Eliot described the subspecies *Discodoris coerulescens* Bergh, 1888 subsp. *variegata* Eliot, 1903. Von Ihering named a species described by Vayssière: *Archidoris stellifera* von Ihering *in* Vayssière, 1903, from the Mediterranean. MacFarland named two new species of *Discodoris* in 1909, including one species dedicated to von Ihering. Finally, in 1924, O'Donoghue named *Discodoris fulva*, from the Pacific coast of Canada.

Three malacologists named new species in the 1930s. Allan named two new species of *Discodoris* in 1932 and 1933, both from Australian waters. Pruvot-Fol named one new species of *Discodoris* based on a specimen collected from Vanikoro by Quoy and Gaimard in 1828. Finally, Baba named two new species of *Discodoris* in 1936 and 1937, both from Japanese waters.

No new species of *Discodoris* were named during the 1940s. Activities started again with White, who named *Discodoris alba* from the Caribbean, in 1952. Starmühlner named *Discodoris cavernae* from the Mediterranean, in 1955. Risbec named *Discodoris notiperda* from the coast of Vietnam, in 1956. More importantly, the 1950s saw the beginning of Ernst Marcus's prolific career as an opisthobranch systematist. In his article on "The Opisthobranchia from Brazil," Marcus (1955) named two new species, *Discodoris evelinae* and *Discodoris pusae*. The 1960s clearly are Eveline and Ernst Marcus' period. In total, they introduced 10 new species names between 1963 and 1967. In 1969, Burn named three new species of *Discodoris*, mainly based on Crawford's collections.

Finally, six new species of *Discodoris* were described after 1979: *Discodoris rosi* Ortea, 1979, from the Atlantic coast of Spain; *Discodoris confusa* Ballesteros, Ortea, and Llera, 1985, from the Canary Islands; *Peltodoris sordii* Perrone, 1990, transferred to *Discodoris* by Cattaneo-Vietti et al. (1990), and *Discodoris patriziae* Perrone, 1991, both from the Mediterranean; *Discodoris achroma* Valdés, 2001, from deep-sea, off New Caledonia; and, finally, a species I recently named *Discodorididae aliciae*, for which I wrote that workers could also use the generic name *Discodoris*, from the Pacific coasts of Mexico and Panama.

Overall, in terms of number of nominal species, the winners are Bergh (26 names), followed by Ernst Marcus (12 names, including eight with his wife), Eveline Marcus (eigth names), Alder and Hancock (six names), and Abraham (five names). This being said, quite a few of those species names are no longer valid. More than half (46) of the *Discodoris* nominal species were named between 1850 and 1910, mainly because of the activities of Bergh, Alder and Hancock, and Abraham. The two decades with the highest number of nominal species named are the 1870s (15 names), especially the year 1877 (11 names), with Bergh and Abraham, and the 1960s (13 names). Only six names of *Discodoris* species were created since 1970.

Combinations

Not all *Discodoris* species names have been originally classified in *Discodoris*, and not all species originally classified in *Discodoris* have remained in it. Of 81 nominal combinations using *Discodoris* as the first part of the binomial, 23 were transferred to *Discodoris* from other genera: *Doris* (15), *Peltodoris* (4), *Archidoris* (1), *Kentrodoris* (1), *Tayuva* (1), and *Zibethina* (1). In total, 58 nominal species were originally placed in the genus *Discodoris*. Prior to the present study, of those 58 names, 18 were transferred to other genera: *Paradoris* (7), *Geitodoris* (3), *Rostanga* (2), *Tayuva* (2), *Asteronotus* (1), *Carminodoris* (1), *Diaulula* (1), and *Platydoris* (1).

None of the new combinations involving a re-allocation to *Discodoris* was supported by any phylogenetic analysis. Some of the new combinations involving a re-allocation from *Discodoris* to another genus were supported by a phylogenetic analysis, such as the transfer of species to *Paradoris* (Dayrat and Gosliner 2005; Dayrat 2006) and *Tayuva* (Dayrat and Gosliner 2005). Some of the other new combinations involving a re-allocation from *Discodoris* to another genus were correct, although not supported by a phylogenetic analysis, such as the transfer of species from *Discodoris* to *Geitodoris*, which is monophyletic. Some other ones, however, were unwarranted and arbitrary, such as the transfer of *Discodoris branneri* MacFarland, 1909 to *Carminodoris* by Perrone and Doneddu (1997).

Number of specimens traditionally used to describe new species

Of the 81 *Discodoris* combinations that exist in the literature, only one name was originally created with more than 10 specimens, *Discodoris pusae* Marcus, 1955, based on 12 specimens. Only three were originally created with more than five specimens (and less than ten specimens): *Discodoris notiperda* Risbec, 1956, based on nine specimens; *Discodoris rosi* Ortea, 1979, based on six specimens, transferred to *Rostanga* by Dayrat and Gosliner (2005); and *Discodorididae aliciae* Dayrat, 2005, based on six specimens. The other 77 names were all introduced based on five specimens or less, and only a single specimen in most cases: five specimens (1), four specimens (3), three specimens (5), two specimens (12), and a single specimen (46); note that we do not know the exact number of specimens used for the original description of 10 nominal species, such as *Discodoris sibogae* Bergh, 1905, and *Doris granulata* Ehrenberg, 1831.

The fact that 56% of the *Discodoris* nominal species have been originally described based on a single specimen has had important consequences on the taxonomy of this group. In particular, many names have been introduced without any knowledge of the infra-specific character variation, which led workers to describe some individual variants of widespread species as distinct species (e.g., *Sebadoris fragilis*). However, not all species names created based on a single specimen have become synonyms or *nomina dubia*: *Paradoris dubia* (Bergh, 1904) or *Paradoris indecora* (Bergh, 1881), two names created based on a single specimen, are regarded as valid (Dayrat 2006). Also, some species described with several specimens actually became junior synonyms: *Discodoris notiperda*, originally described based on nine specimens (the second highest number of specimens used in a *Discodoris* species description in history), is one of the many junior synonyms of

Sebadoris fragilis (Alder and Hancock, 1864). This indicates that, although the lack of information on infra-specific variation is a major issue that often leads to synonymy, other factors also are very problematic, especially the fact that many original descriptions were incomplete anatomically (key organs such as the reproductive system and the radula not described, see below) and taxonomically (no comparison with other existing species).

Anatomical knowledge

Prior to the present study, our anatomical knowledge of *Discodoris* species was poor in most species, with a few exceptions such as *Discodoris boholiensis*, redescribed by Valdés (2002) and *Discodoris pusae* (now, *Geitodoris pusae*) originally described by Marcus (1955). Nearly all original species descriptions are largely incomplete (i.e., at least for the most important key characters, such as the copulatory organs and the radula). Many original descriptions come with no drawing of the dorsal color, no drawing of the reproductive system, no pictures of the radular teeth, etc. Many of Bergh's descriptions (e.g., Bergh, 1876, 1877a, 1877b, 1878a, 1878b, 1879a, 1879b, 1880a, 1880b) are quite detailed, but most details deal with features that are not particularly useful for distinguishing species. Also, the lack of drawings (especially for the reproductive system) makes those descriptions poorly informative, unless a peculiar feature is mentioned. However, when they are illustrated with figures, Bergh's descriptions can be very informative, such as the description of *Hoplodoris desmoparypha* (Bergh 1880a:51-56; Bergh 1905:113-115). Generally speaking, the fact that many species were described based on a single specimen prevented authors from: 1) noticing inconspicuous yet important details, 2) avoiding mistakes, and 3) determining individual variation of anatomical features.

Several *Discodoris* species were redescribed subsequently to their original descriptions. Bergh occasionally redescribed species; for instance, he originally described *Discodoris concinna* in 1888, and then redescribed it in 1890 and again in 1905. However, his re-descriptions were similar to his original descriptions, i.e., detailed but not informative. MacFarland's (1966) monograph includes only one *Discodoris* species (*Discodoris heathi* which actually belongs to *Geitodoris*). Edmunds (1971, 1972) published interesting remarks on the anatomy of the reproductive system, but his work occasionally suffered from misidentifications. More recently, Valdés (2002) redescribed the anatomy of the type species of discodorid genera, such as *Discodoris*, *Peltodoris*, *Geitodoris*, and *Paradoris*. However, Valdés's main goal was to reconstruct the higher relationships within cryptobranch dorids, not to revise the alpha taxonomy of any of the genera, and his re-descriptions were thus based on a single specimen per species.

Finally, infra-specific character variation has seldom been addressed: the variation of the dorsal color of *Peltodoris atromaculata* was studied in detail by Thompson (1985), but little information was available for the rest of the anatomy; Bertsch (1976) elegantly analyzed the infra-specific variation for the radular formula of *Discodoris evelinae*. In the present revision, the infra-specific variation of all characters described is addressed. Unexpected anatomical features become obvious only after many individuals are dissected, and remain unnoticed if only one or a few specimens are examined.

Diagnoses of *Discodoris* and phylogenetic relationships

Two of the most important and revolutionary principles of Hennig (1966) are that: 1) organisms are mosaics of characters (i.e., characters evolve at different rates and therefore must be used at different levels of tree), and 2) not all characters should be regarded as indicators of relationships among species or groups of species (i.e., only synapomorphies tell us something about supra-specific relationships). So 'working in a phylogenetic framework' means that one needs to: 1) Treat characters one by one and realize that each character supports relationships at one particular level in the hierarchy and not at multiple levels (unless it is a multistate or homoplasic character); 2) make a distinction, at each level, between symplesiomorphies (which do not indicate natural groupings) and synapomorphies (which indicate natural groupings).

Those two critical points help produce modern phylogeny-based diagnoses. For instance, a clear distinction can be made between the characters that are found in *Paradoris* species because (Dayrat 2006:1) they are found in many dorids beyond Discodorididae; 2) they are synapomorphies of Discodorididae, and therefore are plesiomorphic at the level of *Paradoris*; 3) they are synapomorphies of *Paradoris*, and therefore are plesiomorphic at the level of *Paradoris* species; and 4) they are found in some *Paradoris* species, but not all, and therefore should not be used as a criterion to re-allocate species to *Paradoris* or remove species from it. Because *Paradoris* is a clade, some features, i.e., the synapomorphies exclusively shared by all species of *Paradoris*, can be used to recognize *Paradoris*.

The main difference between *Paradoris* and *Discodoris* is that *Discodoris*, at least as it has been traditionally delineated, does not correspond to a clade, even after several *Discodoris* species are re-allocated to other discodorid subclades. Indeed, our knowledge of phylogenetic relationships in Discodorididae can be summarized as follows (Dayrat and Gosliner 2005): some discodorid subclades are (more or less) easily recognized and diagnosed based on a few (usually one) key morphological features, such as *Platydoris* (Dorgan et al. 2002), *Jorunna* (Camacho-García and Gosliner 2008), *Halgerda* (Fahey and Gosliner 2000), *Geitodoris* (Schrödl 2000), *Thordisa* (Chan and Gosliner 2007), and *Paradoris* (Dayrat 2006), which all correspond to genus-level taxa traditionally recognized by previous workers; the relationships among those subclades is still unclear; many species (most of which are *Discodoris*, but also *Peltodoris* and *Anisodoris* species) belong to a large metaphyletic group at the base of Discodorididae within which the relationships are unknown –Valdés and Gosliner (2001) found all caryophyllidia-bearing dorids to form a clade within the Discodorididae, but this result is not confirmed in the present study.

This peculiar phylogenetic situation has had some important consequences on diagnoses proposed for *Discodoris*, as well as on how people have used *Discodoris* as a genus name for Linnaean binomials (Dayrat and Gosliner 2005).

Discodoris has been traditionally used as a genus name for species that clearly belong to well-delineated clades, such as *Paradoris* and *Geitodoris*, but were placed in *Discodoris* by mistake. For example, *Discodoris lora* and *Discodoris lilacina* were recently transferred to *Paradoris* and *Tayuva*, respectively, based on phylogenetic analyses (Dayrat and Gosliner 2005; Dayrat 2006); indeed, *lora* belongs to the same clade as the type species of *Paradoris*, and *lilacina* belongs to the same clade as the type species of *Tayuva*.

More importantly, *Discodoris* has also been traditionally used as a genus name for species that could not be placed in any clearly-delineated genus of Discodorididae. As a result, *Discodoris*, and *Peltodoris* and *Anisodoris* as well to a certain extent, have been used as genus names for species that people did not know where to classify. This situation is mainly the result of the fact that many species are actually difficult to classify. Of course, the fact that people were not working in a phylogenetic framework did not help, but several groups that we admit as clades today (*Platydoris*, *Geitodoris*, *Halgerda*, etc.) have been recognized a long time ago, whereas the classification at the genus level of most *Discodoris*, *Peltodoris*, and *Anisodoris* species is far from being obvious. In fact, many *Discodoris* species have been classified in multiple other genera: because many of those species at present belong to a metaphyletic group at the base of Discodorididae, and are hard to classify, have been placed in arbitrary genera.

The case of *Sebadoris nubilosa* illustrates well this situation. Currently classified in *Sebadoris*, it was originally classified in *Doris*, and then transferred to *Discodoris* and *Archidoris*. The combinations available for its synonyms involve other genera: *Thordisa crosslandi*, *Sebadoris crosslandi*, *Diaulula gigantea*, and *Argus indicus*. Also, *nubilosa* was misidentified as *Austrodoris ellioti* (not *ellioti* Alder and Hancock, 1864). So, in total, specimens of *Sebadoris nubilosa* were classified in eight different genera, one of which being *Discodoris*. The case of *nubilosa* is not exceptional in *Discodoris*.

All the diagnoses published so far for *Discodoris* are misleading because they were never based on any phylogenetic analysis. All those diagnoses include characters that are found in all discodorids (e.g., notched upper lip of the anterior foot) or many dorids (e.g., hamate teeth, jaws on the labial cuticle), but no features exclusively present in *Discodoris* (as traditionally delineated) which could be potential synapomorphies. Actually, we shall see that it is possible to use the taxon name *Discodoris* to refer to a clade, but that this clade includes only three species out of the dozens of existing *Discodoris* species names.

MATERIALS AND METHODS

Establishing a List of Species Names

The two primary questions of a taxonomic revision (i.e., which species names are valid, and what are the relationships among species) require sampling two different lists of species. One must not confuse the list of species names established for determining which species names are valid within a given group, and the sample of species for determining the relationships among the species of that group.

One of the first steps in a taxonomic revision of a given group is to establish a list of all species names that belong to that group, i.e., all species names that have been classified within that group or have not been classified in it but should be transferred to it. This first step is absolutely critical because it is the only way one can determine the nomenclatural status (e.g., whether a name is synonymous, valid, or dubious) of the species names of a given group, and therefore evaluate the exact species diversity of that group.

Establishing such a list is relatively easy when the group being revised is monophyletic (e.g., Dayrat 2006). One simply has to look for synapomorphies in types and original descriptions. This can be time-consuming though, because it often requires looking for species that were misplaced. However, this is not necessarily complicated, unless types and original descriptions are incomplete (as often in discodorids). Once this list is established, then one determines which names are valid and which ones are not. Several discodorid taxa traditionally ranked at the generic level are easily recognized, such as *Paradoris* (Dayrat 2006), *Geitodoris* (Schrödl 2000; Dayrat in prep.), *Platydoris* (Dorgan et al. 2002), and *Rostanga* (Rudman and Avern 1989). They are 'good' clades, and establishing a list of species names that belong to them would not be too complicated (although it may be time-consuming). Also, when the group under revision is a clade, it is relatively easy to establish the taxon sample for testing the phylogenetic relationships within that clade: It consists of all the valid names within that clade. There is no need to sample synonyms: for example, for a phylogenetic analysis within *Paradoris*, *indecora* was sampled but its synonyms (*cavernae*, *ceneris*, *granulata*, *inversa*, and *mollis*) were not sampled (Dayrat 2006).

Establishing a list of species names for the revision of a group that is not a clade is more complicated. *Discodoris* has been used as a genus name for species that people did not know where to classify and that, consequently, were often placed in several other genera besides *Discodoris*, such as *Peltodoris* and *Anisodoris*. A comparison between *Paradoris* and *Discodoris* is useful here. The nomenclatural history of *Paradoris*, i.e., the history of all the binominal combinations proposed for *Paradoris* species, is almost exclusively linked to one genus (*Discodoris*) besides *Paradoris* (with the exception of one combination with *Percunas*, and another with *Alloiodoris*). However, the nomenclatural history of *Discodoris* species is linked to a total of 21 generic names: *Alloiodoris*, *Anisodoris*, *Aporodoris*, *Archidoris*, *Argus*, *Asteronotus*, *Austrodoris*, *Carminodoris*, *Diaulula*, *Doris*, *Geitodoris*, *Kentrodoris*, *Otinodoris*, *Paradoris*, *Peltodoris*, *Platydoris*, *Rostanga*, *Sebadoris*, *Aporodoris*, *Tayuva*, and *Zibethina*. This means that dealing with the nomenclatural and taxonomic history of *Discodoris* names required considering the literature of 21 other genera for various reasons.

Here are some of those reasons. (1) Because *Discodoris crawfordi* was transferred to *Rostanga*, it was necessary to check whether *Rostanga crawfordi* was a synonym or a valid name of an already existing *Rostanga* species. It actually is a valid name with two new junior synonyms: *Rostanga australis* Rudman and Avern, 1989, and *Discodoris turia* Burn, 1969. (2) A drawing of the dorsal color published by Abraham (1877) for *Doris murrea* looked similar to the dorsal color of *Discodoris mauritiana* Bergh, 1889, so the type of *murrea* was borrowed, which turned out to be actually identical to *mauritiana*. (3) Lim and Chou (1970) transferred *Kentrodoris annuligera* to *Discodoris*, so it was necessary to check if they had misidentified *annuligera*, or if they just had proposed wrong generic affinities for it.

In summary, because of the peculiar phylogenetic situation in *Discodoris* (i.e., many species are part of a metaphyletic group at the base of Discodorididae) and also because it was used for a long time as a genus for species that people could hardly classify, the nomenclatural history of *Discodoris* involves 21 generic names instead of just two or three.

The list of all potential synonyms of *Discodoris* species was established step by step. First, all the species names (placed in genera other than *Discodoris*) that should probably be considered were identified from the literature, and, second, the types of all species suspected to potentially refer to a '*Discodoris*' species were borrowed and examined. This procedure yielded many new synonymies, such as *Doris raripilosa* Abraham, 1877 as the valid name for *Otinodoris winckworthi* White, 1948, *Hoplodoris desmoparypha* Bergh, 1880, and *Platydoris papillata* Eliot, 1903. It certainly is possible that some names were overlooked and that new valid names might be discovered, in spite of careful investigations.

In total, 119 specific names (many of which were combined with more than one generic name) and six subspecific names are considered in the section on Species Descriptions below. These 125 names include: all specific names placed at least once in *Discodoris* or *Peltodoris*, most specific names placed in *Anisodoris*, and several other specific names placed in other genera such as *Doris* and *Rostanga*. A complete list of those names is provided in Appendix 1.

The taxon sampling for the phylogenetic relationships among *Discodoris* species is discussed below in the phylogenetics section.

Type Material

Sound nomenclatural decisions require re-examining types. For the present study, it was attempted to locate and request all type specimens for all the species names considered (i.e., a total of 119 specific and six subspecific names). However, the type material of 35 species could not be found. All types available were re-examined, with just a few exceptions. In some cases (*Peltodoris fellowsi* Kay and Young, 1969; *Archidoris hawaiiensis* Kay and Young, 1969), the holotype *and* the paratype(s) were requested, but just one paratype was received. In some other cases (*Argus indicus* O'Donoghue, 1932; *Discodoris patriziae* Perrone, 1991; *Discodoris whitleyi* Allan, 1932; *Peltodoris sordii* Perrone, 1990), requests remained unanswered. Finally, the type material of

Peltodoris nayarita Ortea & Llera, 1981 and *Rostanga australis* Rudman and Avern, 1989, needed towards the end of the study, was not requested (because they would not have changed the taxonomic decision). Finally, in the context of this revision, many other types not mentioned here were re-examined, such as all types of *Paradoris* species (Dayrat 2006) and *Geitodoris* species (revision in preparation).

Additional Material

Hundreds of specimens were examined and dissected for the present revision. Many of them are preserved at the California Academy of Sciences (CAS), but most of the non-type specimens that could be located were also requested. Hundreds of specimens were borrowed from the following museum collections: Australian Museum, Sydney (AM); B. P. Bishop Museum, Hawaii (BPBM); Hancock Museum, Newcastle-upon-Tyne, England (NEWHM); Museo Nacional de Ciencias Naturales, Madrid (MNCN); Museu de Zoologia da Universidade de São Paulo (MZSP); Muséum national d'histoire naturelle, Paris (MNHN); Museum of Comparative Zoology, Cambridge (MCZ); Museum of New Zealand, Wellington (MNZ); National Museum of Victoria, Melbourne (NMV); Natural History Museum, London (NHM); National Museum of Natural History (NMNH), Smithsonian Institution; Zoological Museum, Amsterdam (ZMA); Zoological Museum, Berlin (ZMB); Zoological Museum, University of Copenhagen (ZMUC).

Material Preparations

It is crucial to let the readers know exactly how many specimens were actually dissected and how many structures were studied per specimens (Dayrat 2006), because there is a difference between dissecting 40 specimens versus one or two. Therefore, whether a specimen was dissected or simply examined externally is always clearly indicated here. The structures studied (especially through SEM) for each specimen are also always clearly indicated. Specimens that had been dissected prior to the present study were incomplete in most cases (mainly because, unfortunately, people rarely send back the SEM stubs with the material): if so, the missing organs are also clearly indicated in the material description. In addition, SEM stubs were prepared for most specimens, but not all. In order to avoid any confusion, all SEM preparations are listed in Appendix 2.

Hard parts such as radulae and jaw plates, were cleaned in 10% NaOH for a few days, rinsed in clean water for at least a week (water changed regularly), briefly cleaned in an ultrasonic waterbath (less than a minute), sputter-coated with gold-palladium, and examined in a LEO SEM (CAS SEM-laboratory). Soft parts, such as mantle tissue, rhinophores, oral tentacles, gills, and penises, were critical point dried before coating. In total, 1,480 SEM stubs were prepared, which yielded 4,600 pictures. Of course, the plates published here only contain a small fraction of those pictures. However, for each species, efforts were made to illustrate the range of the infra-specific and geographical variation. All SEM stubs prepared for the present study were — or will shortly be — sent back with the specimens to museum collections, so that all observations presented here are repeatable in the future.

Whenever a lot would include more than one specimen, each specimen was carefully labeled, both inside the jar (if organs were separated, then each organ was labeled as well), in the material description published here, and on the stubs, so that future workers will be able to link unambiguously the present anatomical descriptions to identifiable specimens in collections.

Drawings and Observations

Contrary to what some people who despise descriptive work think, anatomical descriptions are difficult to realize. The greatest difficulty probably is to *see* what has not been mentioned by previous workers. Organisms cannot be discovered through a single look, exactly like paintings or landscapes. *Examining* and *seeing* anatomical details takes time, patience, expertise, and is certainly not a passive activity. One needs to pay close attention to minute details, and then track those details in a large number of specimens: it frequently happens that one does not *see* a structure at first, though obvious, but only *sees* it after checking many specimens of the same species, or many times the same individual.

All anatomical drawings produced in the context of the present revision were checked several times at different periods (a single verification per drawing was not sufficient). Not all the drawings presented here are correct (some drawings certainly are inaccurate or incomplete, despite all verifications). However, verifying drawings several times considerably diminished the number of mistakes. Most mistakes found in the literature come from the fact that some workers do not take the time to verify their observations several times.

In most drawings, the positions and shapes of the organs and structures were represented exactly as they were seen, without being moved. In some other drawings, however, some structures were moved or even removed, in which case it is indicated in the legend in order to avoid any confusion. The present study is based on more than 2,000 anatomical drawings. The plates published here only contain a "small" sample of those drawings. However, for each species, efforts were made to illustrate the whole range of the infra-specific character variation.

Plates

Plates include different kinds of pictures and drawings: 1) color pictures representing dorsal and ventral color of live animals; 2) black-and-white or color drawings of the dorsal notum from original descriptions; 3) anatomical drawings; 4) some anatomical drawings from original descriptions redrawn here; 5) SEM pictures. Plates are organized by species and then by organ, with the exception of a few problematic specimens of *Tayuva* cf. *lilacina* for which plates are specimen-based. Also, because types have a special status in taxonomy, special plates are made for types (including drawings from original publications): pictures and drawings of types are separated from the rest of the material, whenever many drawings and pictures were available; otherwise, when few illustrations were available, (type and non-type) figures are kept on one or two plates.

Anatomical Abbreviations

a	anus	lsg	left salivary gland
abg	anterior blood gland	mg	mucous gland
ag	accessory gland	mw	muscle wall
amp	ampulla	ot	oral tube
bc	bursa copulatrix	pbg	posterior blood gland
bm	buccal mass	pr	prostate
c	caecum	rcpg	right cerebro-pleural ganglia
cnr	circum-esophageal nerve ring	rds	radular sac
dd	deferent duct	rgm	right ganglionic mass
dg	digestive gland	rps	reproductive system
e	esophagus	rrg	right rhinophoral ganglia
fd	fertilization duct	rs	receptaculum seminis
fgm	female gland mass	rsd	receptaculum seminis duct
i	intestine	rsg	right salivary gland
lcpg	left cerebro-pleural ganglia	ss	stylet sac
lgm	left ganglionic mass	st	stomach
lrg	left rhinophoral ganglion	vd	vaginal duct

Literature

Original descriptions (and, when available, redescriptions of originally poorly-described types) clearly are the most important literature in taxonomy. For that reasons, original descriptions of all species names (including synonyms) are commented on. In addition, all the contributions that could be found on all species names were read, as well as many other contributions for various purposes (e.g., additional data on out-groups). Some contributions, especially field guides or checklists, might have been overlooked. However, the vast majority of contributions containing anatomical data are cited. On the one hand, the literature is a great source of information (for distribution, character variation, etc.). On the other hand, anatomical descriptions published in the literature should not be taken for granted, because many species are misidentified. For example, the use of species names such as *Discodoris concinna* and *Discodoris fragilis* has been extremely confusing and many papers where those names appear can hardly be used because we ignore which species they actually refer to. Some mistakes found in the literature could occasionally be corrected (if material studied by previous authors was available).

Species Descriptions

All species descriptions include the following sections: A list of species names with all bibliographic references; Type material; Type locality; Type material condition; Additional material dissected; Additional material examined (not dissected); Distribution; www; Occurrence; Habitat; Literature; Remarks on the original description(s); Description of new specimens; Diagnostic features; Infra-specific character variation; Discussion; Supra-specific relationships; Future studies.

All references found are listed in the 'List of species names' section, except for the cases interpreted as misidentifications, which are discussed in the literature or the discussion sections. Misidentifications are also mentioned in the distribution section, in order to avoid any confusion.

The type material section provides a detailed description of the type material, i.e., where it is currently preserved and whether it is publicly available or not (a few types could not be borrowed although they were apparently deposited in a public institution). The 'type material' includes the type specimen(s) or what remains of it (them) in the jar, e.g., an empty body wall with all internal organs missing) as well as all the organs that have been prepared by previous authors: the radula and the labial cuticle on SEM stubs, the reproductive system in a small vial inside the jar or on a histological slide, etc. Also, the correct status of the types is mentioned in this section: e.g., whether the designation of a holotype and (a) paratype(s) on museum labels is invalid, because not fixed in the original publication and by the original author(s) (*ICZN*, Article 73.1.3). Many types of the NHM, London, were wrongly designated as holotypes and paratypes (the mention 'holotype' and 'paratype' was inappropriately added on labels of syntypes). Finally, in order to avoid confusion, any piece of information or comments that were not written on the labels of the specimens are indicated between brackets. For example, the type material of *Discodoris alba* White, 1952 reads: "Holotype (NHM 1934.9.11.105), by monotypy: one specimen 32/15 mm preserved, leg. G. Tandy and J. S. Colman, [no collecting date]." The mention "[no collecting date]" means that the label and the original description do not indicate when the material was collected.

The type locality of a species is the locality of the type(s) with a name-bearing function, i.e., holotype, lectotype, neotype, syntypes (*ICZN*, Article 76). In the type locality, the localities of the rest of the original material, i.e., the types with no name-bearing function (paratypes and paralectotypes), are also indicated, although they are *not* part of the type locality. Any piece of information that is not on the label (including information that was published in the original description but was not written on the label) is indicated between brackets. For example, the type locality of *Doris* *sordidata* Abraham, 1877, a new replacement name for *Doris sordida* Quoy and Gaimard, 1832 reads: "Ilots aux cerfs, île de France [Mauritius, Indian Ocean];" the Ilots aux cerfs is in Mauritius, but this information is *not* mentioned on the label of the type material.

The condition of the type material is rarely described by authors. However, this is critical information because some types may be available but uninformative. For example, it is not rare to find types that dried for a while and were put back in alcohol, in which case they are usually dark brown and completely destroyed (except for the jaws and radulae, if still present). More importantly, some authors seem to consider that just the body wall is part of the type material and thus do not deposit their anatomical preparations (including slides and SEM stubs). This is a real problem because a type deposited without the SEM stub of the radula and without the reproductive system in a small tube is almost as uninformative as no type at all. Also, some authors who re-examine types and mount a radula on a SEM stub send back the body wall of the specimen but often keep the SEM stub. Such practices are not acceptable and are based on a regrettable ignorance of the priceless, crucial value of types.

The specimens dissected are listed as additional material dissected, and the specimens simply examined externally are listed as additional material examined. For every specimen, is indicated: the locality, the collecting date, the specimen size (length/width in mm), the collector(s), the identification (as written on the label), the name of the identifier, and the catalogue number. In order to avoid confusion, any information that was not on labels is indicated between brackets, along with any information on the condition of the specimen, i.e., whether the specimen was opened prior to the present study, whether some organs were missing, etc. Material data thus read as follows: "Australia, Victoria, Philip Island, Kitty Miller Bay, [no collecting date], one specimen 20/12 mm preserved, [leg. unknown, probably R. Burn], identified as *Discodoris dubia* by R. Burn (NMV F21247) [R. Burn originally identified this species as *Alloiodoris nivosus*; this specimen was opened dorsally prior to the present study]."

Species distribution is based on the specimens that were studied in the context of the present monograph as well as the literature. However, all contributions where species were misidentified are excluded. Cases where distribution records should be regarded as uncertain too (because of uncertain identification) are also indicated.

The *World Wide Web* is an important source of information. In particular, it provides us with invaluable distribution records for species easily recognizable with their dorsal color. In the *www* section, all records regarded as correct (whether the species were correctly identified or misidentified) are mentioned. Identifications that seem to be incorrect (although it is often difficult to have an opinion without being able to dissect the individuals) are also discussed. Of all the sea-slug sites available on the *Web*, Bill Rudman's fantastic *Sea Slug Forum* needs a special mention: although it is not peer-reviewed *per se*, it is interactive, which means that anybody can send an e-mail to correct any identification, a process that considerably enhances the quality of the systematics of the website.

In the species occurrence, it is attempted to summarize how many specimens are known for each species, i.e., how many specimens were mentioned in the literature, how many are available in collections, etc. The species habitat section provides data on the habitat species have been found to live in.

The literature available for each species is commented on: the reader can learn where to find anatomical data, distribution data, etc. Incorrect identifications found in the literature are also mentioned in this section.

All remarks on the original description are based on re-examination of the type material (when available) and the text of the original description as well. They exclusively concern the type material, with a distinction between the holotype and the paratype(s) or between the different syntypes when appropriate. More particularly, this section is used to correct mistakes published in the original description and to add new observations.

The descriptions of new specimens are based on non-type, additional specimens dissected in the context of the present monograph. Those descriptions go through the entire anatomy (color, external morphology, digestive system, nervous system, reproductive system). The infra-specific variation of all characters is also emphasized.

In the diagnostic features, all the (autapomorphic) features that could be used to identify species are listed. Those diagnostic features may be external characters (e.g., color) or internal, anatomical details (e.g., penis morphology). Note that most diagnostic features do vary infra-specifically, but they vary within a certain range that does not overlap with other species.

In the infra-specific character variation, all the data on infra-specific variation available from the literature (with misidentifications taken out) as well as new observations are synthesized. However, most data on infra-specific variation are based on new observations since it is the first time that so many specimens are dissected for the targeted purpose of addressing individual variation.

The discussion reviews what previous authors have written about each species (including synonyms). In particular, misidentifications as well as doubtful identifications are discussed. The status of species names (valid name, synonym, or *nomen dubium*) is also discussed. The supra-specific relationships of each species are presented in a separate paragraph, after the discussion.

Finally, when appropriate, interesting and important questions that could be addressed in future studies are briefly mentioned. Many of those questions are potential subjects for future research projects (future studies are also mentioned in the discussion as well).

The Use of the Term 'species' and Species Delineation Criteria

All species considered in this monograph are morphospecies: species exclusively supported by morphological data. They consist of a set of individuals that share a similar anatomy (acknowledging that some features may vary among individuals), with at least one diagnostic feature that distinguishes them unambiguously from all other species. Such diagnostic features can be used as clear-cut criteria for identification purposes. For example, the peculiar dorsal color of *Peltodoris atromaculata* can hardly be confused with any other species. However, in the case of *Tayuva*, species could not be delineated unambiguously. Because *Tayuva lilacina* likely includes more than one species, it is treated here as a species complex.

Also, in some cases (e.g., *nomina dubia*), the term 'species' is used to refer to what the *ICZN* calls 'nominal species,' i.e., species whose existence is limited to a name attached to one (or several) type(s). However, nominal species really are species names rather than species as biological entities, because the only information we have about nominal species is a name on the label of a specimen (or in many cases just the original description and nothing else).

As many specimens as possible were dissected for each species described in the species description section. A large sample size is the only way one can address properly infra-specific character variation and determine whether or not a group of individuals share a diagnostic feature. The core of species delineation consists in a detailed study of the infra-specific variation of all characters potentially useful at the species level. Delineating species based on morphological characters without addressing the individual variation of those characters is bad science.

Apart from the fact that studying individual variation is key in species delineation, it is difficult to describe the series of steps followed to delineate species. Indeed, it implies to continuously go back and forth from one specimen to another, from one character to another, from new observations to the literature, from the types to the non-type specimens, etc., until a group of individuals all part of a species can be determined. This long process often implies to change our mind repeatedly.

Identifications on labels in museum collections are not an issue in cases where species are easily recognizable and have never been confused, such as *Peltodoris atromaculata* and *Discodoris boholiensis*. However, identifications can be misleading in cases where species have been poorly recognized. For example, the use of names such as *Discodoris concinna*, *Discodoris fragilis*, and *Sebadoris nubilosa* has been largely inconsistent among museum collections and even within each collection. The name *Discodoris fragilis* has been used for specimens regarded here as members of five different species (*Discodorididae coerulescens*, *Sebadoris fragilis*, *Tayuva lilacina*, *Peltodoris murrea*, and *Asteronotus raripilosa*); *Discodoris concinna* for specimens of three different species (*Sebadoris fragilis*, *Tayuva lilacina*, and *Peltodoris murrea*); and *Sebadoris nubilosa* for specimens of three different species (*Sebadoris fragilis*, *Tayuva lilacina*, and *Sebadoris nubilosa*); etc. Because it was not possible to know in advance whether or not identifications were correct, no identification was taken for granted. Note that, on occasion, this problem would also occur with type material. For example, the type material of *Discodoris notha* includes two syntypes that are part of *Discodorididae branneri* and two syntypes that are part of another entity, *Discodorididae notha*; one of the two syntypes of *Discodoris rubra* actually is part of *Sebadoris fragilis*. Such cases were solved by the designation of lectotypes.

Nomenclatural Guidelines

Form of species names

Throughout this monograph, not all species names are strictly Linnaean, i.e., based on a combination of a generic name and a specific name. This is related to the fact that this monograph is being written at a period of important, nomenclatural debate. Indeed, the *PhyloCode*, or *International Code of Phylogenetic Nomenclature* (*ICPN*), is scheduled to be published shortly. An article governing species names was recently added in the *PhyloCode* (see, Dayrat et al. 2008). In the context of the *ICPN*, it is no longer mandatory to cite a generic name before a specific name, i.e., supra-generic taxon names can be combined with specific names when no generic name referring to a clade can be found. The advantage of this approach is that all the species that belong to the metaphyletic group at the base of *Discodorididae* can be referred to as, e.g., *labifera* Abraham, 1877 or *Discodorididae labifera* Abraham, 1877, without having to be forced to classify *labifera* within a taxon of genus-rank, because the first higher clade *labifera* belongs to is *Discodorididae*. Note that, under the *ICPN*, higher clade names are all italicized, including all names referring to supra-generic names under the rank-based codes. For that reason, *Discodorididae* is italicized in the present work.

However, both the valid *ICZN* binomials and the *ICPN* species names are mentioned for every species. For instance, the description of *labifera* opens with two names: *"Montereina" labifera* (Abraham, 1877) and *Discodorididae labifera* (Abraham, 1877). "*Montereina*" is a generic name that does not refer to a clade but complies with the *ICZN*. Throughout this monograph, species are refered to by a specific name only (e.g., *labifera*) when there is no risk of confusion (as in the description of *Discodorididae labifera*), and by a binominal *ICPN* name (e.g., *Discodorididae labifera*) when there is risk of confusion about classification (e.g., when comparing *Discodoridae labifera* with *Sebadoris fragilis*). Finally, for some species, the supra-generic name *Doridina* (to which *Discodorididae* is subordinated) for all the species that could only be placed within *Doridina* and that may or may not belong to *Discodorididae* (see, the special section on 'species that may or may not belong to *Discodorididae*' in Species Descriptions).

Note that the section on Species Descriptions is organized taxonomically, i.e., phylogenetically: all *Discodoris* species follow each others, all *Peltodoris* follow each others, all *"Montereina"* species follow each others, etc. Within each supra-specific taxon, species are organized alphabetically. This should help the reader to find a species description within the monograph.

Creation of new species names

No new species name is proposed in this monograph. However, several species are described as new. The main reason for describing but not naming new species is that important data were missing (e.g., no information on the dorsal color of live animals). However, those potentially new species are partially described here so the community is aware of their existence (Dayrat 2005b). They can be formally named whenever those species are better known, i.e., when new specimens are made available.

Nomenclatural status of species names and *nomina dubia*

When types and/or original descriptions do not provide any information that could help us re-identify the species they refer to, then it is appropriate to regard a species name as a *nomen dubium*. Even if new material were to be available from the type locality, there would be no way to determine that the name that is a *nomen dubium* applies to this new material. Here, several species names are regarded as *nomina dubia*. The status of *nomen dubium* was adopted in a conservative way, i.e., in restricted cases. In particular, a distinction was made between *nomina dubia* and names that refer to poorly-known species due to under-representation in collections. Indeed, many regions have been poorly explored, such as the Caribbean Sea, and so there is no need to regard a name as a *nomen dubium* just because non-type material is not available, especially when some features in the original descriptions could help future re-identifications. Therefore, when trying to determine the status of the species names, four categories were distinguished: valid names of well-known species; synonyms of well-known species; potentially valid names of poorly known species; names of doubtful application (*nomina dubia*).

Designation of lectotypes and neotypes

In all cases where syntypes did not belong to the same entity (such as in *Discodorididae notha* and *Discodorididae rubra*), a lectotype was designated. No lectotype was designated if all syntypes are part of the same entity. When no name-bearing type specimen is available, a neotype can be designated (*ICZN*, Article 75). No neotypes were designated here, however, because additional specimens were poorly preserved or not collected from type localities.

Cladistic Analyses

Taxon sampling

The aim of the cladistic analyses was to address the relationships among the basal discodorids, especially *Discodoris*, *Peltodoris*, and *Anisodoris* species. However, those taxa do not form a monophyletic group (at least in their traditional delineation). Therefore, additional discodorid species were selected in order to establish a taxon sample that would be more representative of the discodorid diversity. In particular, additional species were selected in taxa with which some '*Dis-*

codoris' species would share similarities: for example, *Discodoris crawfordi* shares some synapomorphies of *Rostanga*, so *Rostanga* species were sampled in order to test whether or not *crawfordi* was nested with them in the *Rostanga* clade. The reader can find explanations and information on the additional species sampled in a previous publication (Dayrat and Gosliner 2005): those additional species represent the following traditional genera: *Asteronotus*, *Carminodoris*, *Diaulula*, *Geitodoris*, *Jorunna*, *Paradoris*, *Platydoris*, *Rostanga*, *Aporodoris*, and *Thordisa*. Finally, eight outgroups were sampled, all external to discodorids (see, Dayrat and Gosliner 2005).

The other issue that needed to be dealt with was that related to *nomina dubia* and the poorly-known species. For both categories, our anatomical knowledge is limited, which tends to introduce many question marks in data matrices. Therefore, multiple cladistic analyses were performed, with and without *nomina dubia* and/or poorly-known species. By doing so, the goal was to address the supra-specific relationships of all species, including all *nomina dubia* and poorly known species without introducing too much noise in the analyses due to the many questions marks of *nomina dubia* and poorly known species. Multiple analyses were performed with different taxon samples, many of which are not reported here. I mention here the taxon samples that yielded informative results (outgroups sampled in all analyses):

Analysis #1. All valid species names, no nomina dubia, no poorly known species.

Analysis #2. All valid species names, all *nomina dubia*, all poorly known species.

Analysis #3. All valid species names, no *nomina dubia*, all poorly known species except for species for which characters #1 and #2 are unknown, i.e., *edwardsi*, *rubescens*, and *stellifera*.

Analyses #4 to #6. All valid species names, no *nomina dubia*, no poorly known species except for *edwardsi* (#4), *rubescens* (#5), and *stellifera* (#6). Analyses #4 to #6 are identical to analysis #1 with only one additional taxon.

Analysis #7. All valid species names, all *nomina dubia* except those for which characters #1 and #2 are unknown (i.e., *angulata*, *maculosa* Cuv., *noumeae*, *patriziae*, *schmeltziana*, *sordii*, *testudinaria*, *timorensis*) or plesiomorphic (*versicolor*), and no poorly known species.

Analysis 7bis. All valid species names, all *nomina dubia* except for those for which characters #1 and #2 are unknown (i.e., *angulata*, *maculosa* Cuv., *noumeae*, *patriziae*, *schmeltziana*, *sordii*, *testudinaria*, *timorensis*), and all poorly known species, except for those for which characters #1 and #2 are unknown (i.e., *edwardsi*, *rubescens*, and *stellifera*).

Analyses #8 to #16. All valid species names, no *nomina dubia* except for *angulata* (#8), *maculosa* Cuv. (#9), *noumeae* (#10), *patriziae* (#11), *schmeltziana* (#12), *sordii* (#13), *testudinaria* (#14), *timorensis* (#15), and *versicolor* (#16), no poorly known species. Analyses #8 to #16 are identical to analysis #1 with only one additional taxon.

Analysis #17. As analysis #1, with *millegrana* (poorly known species) added, to test whether or not it is nested with *Taringa* species.

Analysis #18. As analysis #1, with *rubens* (*nomen dubium*) added, to test whether or not it belongs to *Geitodoris*.

Analysis #19. As in analysis #1, with *tristis* (*nomen dubium*) added, to test whether it belongs to *Platydoris*.

Analysis #20. As in analysis #1, with *tristis* (*nomen dubium*) added, to test whether it belongs to *Platydoris*, and with the coding changed for character #8 (lobes present instead of unknown, i.e., present or absent, as in the main data matrix)

Characters

The list of characters used is given below. Detailed information about each character can be found in the special section on infra-specific character variation, the species descriptions, as well as in Dayrat and Gosliner (2005). The complete data matrix is given in the Appendix 3.

#1- *Anterior margin of the foot*. The anterior margin of the foot is bilabiate in all the taxa taken into account. The upper lip can be notched in the median line. The notch is absent (0) or present (1).

#2- *Oral tentacles*. Oral tentacles have a narrow basis and are clearly distinct from the tegument of the mouth lips; they are placed between the foot and the inferior mouth lip; they can be digitiform or flattened, grooved or not. Oral tentacles are found in all *Discodorididae*. Oral tentacles are auriculate, i.e., not digitoform (0), digitiform (1), or absent, with naked mouth lips (2).

#3- *Oral tentacle groove*. Oral tentacles can be grooved (1) or not (0).

#4- *Body shape*. The body can be more or less elevated or depressed (0) or significantly flattened (1).

#5- *Tubercles*. The dorsal notum of *Discodorididae* is usually covered by tubercles. The most common tubercles are more or less conical, rounded or pointed, with protruding spicules. Some tubercles, with a distinct shape, are treated as distinct apomorphic states. The notum can be finely granular with low and well-spaced tubercles, such as in *Paradoris indecora*; The notum can also be covered by large tubercles, such as in *Carminodoris estrelyado*. Tubercles are more or less conical, rounded or pointed (0), low and well-spaced (1), or large and flat (2).

#6- *Long conical papillae*. The notum can bear long conical papillae. Papillae are not homologous with tubercles because specimens may bear both tubercles and papillae. A primary homology is assumed between long papillae found in *Thordisa* and *Aporodoris* species, as well as *Discodorididae aliciae*. Long conical papillae are absent (0) or present (1). In *aliciae*, they are surrounded by smaller papillae arranged in circles (2).

#7- *Spicule arrangement*. Some tubercles called 'caryophyllidia' are specialized structures (e.g., Foale and Willan 1987; Gosliner 1994; Valdés and Gosliner 2001) characterized by a crown of spicules that surrounds a ciliated apex. However, all caryophyllidia are not identical. They can have a long, narrow peduncle (as in *Jorunna*), be simply conical (as in several species described here), or be low with their crown of spicules almost laying on the notum (as in *Platydoris*). The spicules can be free from the base of the peduncle up to the apex, or embedded within the peduncle for part of their length. Spicules can protrude on the surface of the tubercles without any particular order, or be arranged in a regular crown of usually less than 10 spicules. The crown of spicules is absent (0) or present (1).

#8- *Gills sheath*. In some species, the gill sheath forms large triangular expansions that may completely close the gill pening. This arrangement results in what is usually called a star-shaped or lobate gill opening. The latter is absent (0) or present (1).

#9- *Dorsal mantle holes*. Two distinct kinds of holes were found in the external mantle (see Dayrat and Gosliner 2005; Dayrat 2006): small holes, usually below 10 µm, and much wider holes, with a diameter of at least 20 µm (usually around 50 µm), which seem to be openings of mantle secretory glands. Wide holes are absent (0) or present (1).

# 10- *Muscular layer underneath the dorsal mantle*. In most species, the dorsal mantle is in a single layer of mantle plus, underneath it, a layer of muscles mixed with connective tissue. In two species (*fragilis* and *nubilosa*), I observed that the thin dorsal mantle could be separated easily from a thick, internal muscular layer (at least in the median part of the dorsal notum). This separation is absent (0) or present (1).

#11- *Labial cuticle*. The cuticle is smooth (0), bear one pair of symmetrical jaws (1), or bears one pair of symmetrical jaws and an additional, ventral jaw (2).

#12- *Shape of the radula*. Most radulae are more or less square or rectangular: their length never equals more than two or three times their width which implies that the number of rows is either about the same as the number of teeth per half row (or inferior to it). Some radulae are significantly elongated: their length equals at least three times their width, and the number of rows equals at least twice the number of teeth. Radulae are rectangular or square (0) or significantly elongated (1).

#13- *Rachidian space*. In most radulae, the half rows on either side of the rachis are close to each other, in which case the rachidian space is narrow. In two species (*Peltodoris fellowsi* and sp. B), I found that the rachidian space was significantly wide (as wide as each lateral side of the radula). The rachidian space can be narrow (0) or wide (1).

#14- *Orientation of rows*. The half rows of teeth are more or less perpendicular to the rachidian axis (0) or arranged at an angle exceeding 45 degrees (1).

#15- *Base of the lateral teeth*. The upper margin of the base of lateral teeth can be concave (0) or convex (1).

in which case it is significantly higher, as in *Asteronotus cespitosus*. This is feature is striking in the innermost teeth.

#16- Size of innermost teeth. The innermost teeth are slightly smaller than the median teeth (0) or dramatically smaller than them with an abrupt transition in size (1).

#17- Hook of lateral teeth. The hook of the hamate, lateral teeth found in discodorids can be of the basic, common type (0), or significantly elongated and slightly less curved, as in *Discodoris boholiensis* (1).

#18- Innermost tooth spur. The innermost lateral tooth can bear an inner strong spur with up to three distinct denticles, as in *Discodoris boholiensis* and *Discodoris cebuensis*. Although an inner spur can be found in other species than *boholiensis* and *cebuensis*, the spurs found in those two species are nearly identical and quite distinct. The *boholiensis*-type inner spur is absent (0) or present (1).

#19- Slender lateral teeth. Lateral teeth can be simply hamate, as in most species. They can also be slender and elongated, in which case the radula (or part of it) is hair-like. Either all the lateral teeth or only some outermost teeth are slender and elongated. Slender and elongate lateral teeth are absent (0) or present (1).

#20- Tooth groove and radular asymmetry. The hook of the teeth can be smooth or grooved on its inner edge. The upper lip of the groove can be significantly expanded (only on the left side of the radula, which results in physical asymmetry). The external lateral tooth groove is absent (0), present (1), present with an asymmetrical expansion of the lip (2).

#21- Spatulate outermost lateral teeth. Outermost lateral teeth are simply hamate (0) or spatulate and tightly attached onto one another (1).

#22- Pectinate outermost lateral teeth. Outermost lateral teeth are simply hamate (0) or pectinate with a comb-shaped tip (1).

#23- Lateral denticles. The hook of lateral teeth is smooth (0) or bears flattened, outer denticles (1)

#24- Caecum size. In dorsal view, the caecum of the stomach can be of moderate size (0) or significantly larger (1).

#25- Intestinal loop. The intestine can be dorsal and straight from the stomach up to the anus (0) or be convoluted, with a long loop on the right, ventral side of the digestive gland (1).

#26- Muscular wall around the atrium. In *Tayuva*, the atrium is protected by a muscular wall. The shape and position of the muscular wall vary among individuals of the same species. The muscular wall is absent (0) or present (1).

#27- Distal accessory glands. Unarmed, distal accessory glands are absent (0) or present (1).

#28- Accessory gland with a hollow spine. Some accessory glands contain a hollow spine. The latter can be straight or curved, with a narrow or wide basis. It ends by a hole which most likely helps convey some glandular secretion. Accessory gland with a hollow spine is absent (0) or present (1).

#29- Stylet sac of 'tomentosa' type. The stylet sac found in *Jorunna tomentosa* is easily recognizable by its two portions, a proximal, tubular, glandular portion, and a distal portion containing a needle-like, solid, straight or curved stylet. The stylet-sac of '*tomentosa*' type is absent (0) or present (1).

#30- Stylet sacs of the 'indecora' type. The stylet sacs hosting a needle-like, solid, straight stylet as in *Paradoris indecora* are easily recognizable. They are absent (0) or present (1).

#31- Prostate. The prostate can be tubular and homogeneous (0), globular and homogeneous (1) or flattened and divided in two parts (2) or three parts (3).

#32- Proximal part of the deferent duct. The proximal part of the deferent duct can be similar to the distal part (0) or significantly wider and folded internally (1).

#33- Penis. A penial cuticle of *Aporodoris aivica* type is absent (0) or present (1).

#34- Vaginal surface. The inner surface of the distal portion of the vaginal duct is usually smooth (0) or armed with hooks (1).

#35- Blood glands. There is a single large blood gland (0), covering entirely the cerebral ganglia, or two separate blood glands (1) anterior and posterior to the cerebral ganglia.

Parsimony analyses

The data matrix was edited in MacClade 4.0 (Maddison and Maddison 2000). Heuristic tree searches were performed in PAUP* 4.0b (Swofford 2000) using a Power Mac G4, and following random stepwise-addition sequence (100 replicates) and tree-bisection-reconnection (TBR) branch-swapping options. Characters were all treated as unordered, undirected, and unweighted. Support of clades was assessed by Bremer support analyses (Bremer 1994) with the same settings as in the general tree searches. Character transformations in the strict consensus tree were viewed with MacClade.

RESULTS

Infra-specific Character Variation

The variation of many features observed during this study is reviewed here. This overview of infra-specific character variation is based on the examination of hundreds of specimens. It is more specifically based on species for which many specimens were dissected, i.e., *Tayuva lilacina* complex (100 specimens dissected, 63 from the Indo-West Pacific, 23 from the eastern Pacific, 7 from the Caribbean, 7 from the Mediterranean and eastern Atlantic), *Sebadoris fragilis* (98), *Discodorididae branneri* (27), *Discodoris boholiensis* (17), *Discodorididae aurila* (14), *Peltodoris murrea* (12), *Discodorididae coerulescens* (11), *Discodoris cebuensis* (11), *Discodorididae mortenseni* (10), *Peltodoris atromaculata* (10), *Asteronotus raripilosa* (9), *Sebadoris nubilosa* (8), and *Discodorididae rubra* (8). Results on the infra-specific variation in *Paradoris* were already presented (Dayrat 2006), and a revision of *Geitodoris* (in preparation) will provide some infra-specific variation specific to that clade. However, most observations in different groups of discodorids yield similar results in terms of infra-specific variation.

Color

The color (both dorsal and ventral) is critically important in nudibranch taxonomy, not only because it provides potentially good diagnostic characters, but also because it often is the only information provided in field guides, and thus the only information used by a large community of people to identify species. Therefore, it is important to evaluate color variation among individuals.

Most often, species tend to have a diagnostic dorsal color. This is with the exception of species that are difficult to distinguish because of a similar dorsal color, such as the *Tayuva*, which has a creamish-greyish dorsal background with darker blotches, and the *Rostanga* species, many of which are bright red-orange. At this stage, the dorsal color is unknown in quite a few species (e.g., *Discodorididae labifera*, *Doridina prea*). Also, the individual color variation is unknown in many species (e.g., *Discodorididae branneri*, *Peltodoris fellowsi*, *Discodorididae greeleyi*, *Discodorididae lancei*, *Discodorididae mortenseni*). In fact, there are only a few species for which color variation is well understood. This includes species for which the color variation has been documented for a long time, such as *Discodorididae nobilis* and *Peltodoris atromaculata*, as well as several species redescribed here, such as *Discodoris cebuensis*, *Discodorididae coerulescens*, *Sebadoris fragilis*, and *Peltodoris murrea*.

Some generalizations about the infra-specific variation of the color can be proposed and discussed. First of all, the ventral and dorsal color varies among individuals in nearly all species (although a species whose dorsal color is homogeneously white may not vary). However, color varies within precise limits, so that each individual retains the diagnostic characteristics of the species to which it is referred. One of the most famous examples in discodorids surely is *Peltodoris atromaculata*, which has never been misidentified in the literature although its dark blotches on the dorsal notum vary a great deal, both in number and size.

Generally speaking, dorsal or ventral dots, spots, or blotches tend to vary a great deal in size and number. The arrangement of those dots and blotches may be diagnostic, however. It is worth pointing out that the terms 'dots,' 'spots,' and 'blotches' are not specific, and often hide distinct kinds of pigmentation. For instance, *Peltodoris murrea* and *Discodorididae coerulescens*, two species with a "spotted" dorsal notum, have often been confused in the past, although their pattern of pigmentation, when examined in detail, is distinct: *Peltodoris murrea* is easily recognizable because of its grayish-pinkish, marble-like background with a few brown dots.

Also, some details of the dorsal color may be found in all animals, regardless of color individual variation. Species such as *Discodoris boholiensis*, *Discodorididae coerulescens*, *Peltodoris murrea*, and *Discodorididae rubra*, have a dorsal notum that varies a great deal but all specimens share similar details: for example, some white tubercles of the dorsal notum of *Discodorididae rubra* bear a distinct black spot at their apex, which cannot be confused with other species.

The only way to identify species-diagnostic details is the examination of many specimens, as many as possible. By definition, a single individual cannot provide us with this key information. Distinguishing species becomes much easier once infra-specific variation is (better) known. The confusion over specific names such as *lilacina*, *fragilis*, and *concinna* has remained one of the most problematic taxonomic issues in discodorids: the present study shows that the ventral surface of *lilacina* only bears small brown dots, whereas the ventral surface of *fragilis* is significantly darker, with large spots and blotches. Also, knowing the color variation helps decide whether or not a species may be new: it can be reasonably proposed that *Discodoris* sp. A is a new species because, although its dorsal notum shares some characteristics of the notum of *Discodoris cebuensis*, it differs from it for some important details.

Finally, the color of preserved specimens is another difficulty that we often have to deal with. Most animals loose their color when preserved. There are a few exceptions, such as *Peltodoris atromaculata*, whose holotype described by Bergh in 1880 has a dorsal color still perfectly recognizable. Although preserved specimens tend to become colorless over time, they may remain informative. Indeed, some pigmentation may remain, such as the ventral dark areas in *Sebadoris fragilis*, which can be used to distinguish *Sebadoris fragilis* from *Tayuva lilacina*.

External morphology

The morphology of the dorsal notum is also critical in discodorid taxonomy, mainly because some discodorids bear caryophyllidia, whereas some others do not bear caryophyllidia. The way we currently define caryophyllidia is problematic because there seems to be several kinds of caryophyllidia. This definition is particularly important because the presence of caryophyllidia is the only (morphological) synapomorphy proposed so far for the caryophyllidia-bearing dorids (Valdés and Gosliner 2001). There is no evidence that a particular species could include animals both with and without caryophyllidia. Therefore, it is reasonable to write that, as of today's knowledge, a discodorid species either bears or does not bear caryophyllidia.

The problem is that, in practice, it sometimes is difficult to decide whether or not tubercles are caryophyllidia. Indeed, when a small number of individuals is available, or when specimens are poorly preserved, it is difficult to determine whether caryophyllidia are present or absent. Also, some animals whose dorsal tubercles are not caryophyllidia may have some isolated tubercles that look like caryophyllidia (all the protruding spicules form a regular crown around the apex of the tubercle). This is quite common in *Tayuva*. Reciprocally, some animals whose dorsal tubercles are caryophyllidia may have some isolated tubercles that do not look like caryophyllidia (with protruding spicules arranged in more than one crown around the apex of the tubercle). This occurs more rarely than the opposite situation, but it was encountered it in several species, such as *Discodorididae aurila* and *Discodorididae* sp. D.

In some cases, the individual variation in the dorsal morphology is misleading. The shape of the dorsal tubercles, for instance, has been used by many systematists. In particular, people have tried to distinguish *Sebadoris fragilis* from other similar-looking species based on whether the dorsal tubercles had a 'pointed' or a 'rounded' apex (see, *Sebadoris fragilis*). In most cases, however, this distinction is useless because many individuals bear both pointed and rounded tubercles. Also, the form of dorsal tubercles may change naturally (depending on the retraction of the dorsal mantle), not to mention that preservation may affect the shape of the tubercles.

Although the shape of dorsal tubercles varies a great deal infra-specifically, there are some distinctive patterns: an individual with a few large, rounded tubercles that can be counted easily can hardly be part of the same species as an individual with many tubercles that cannot be counted easily. This implies that, in spite of infra-specific variation, the shape of the dorsal tubercles can be useful at specific and supra-specific levels. Two examples of diagnostic dorsal tubercles are found in *Sebadoris nubilosa*, with long, soft tubercles, and *Discodorididae aliciae*, with long, large papillae surrounded by crowns of secondary papillae of smaller sizes. Other species with similar tubercles are likely to be found in the future. One example of dorsal tubercles potentially useful at the supra-specific level are the *indecora*-like round tubercles found in some *Paradoris* species (Dayrat 2006). The dorsal notum of some species bears some structures in addition to the tubercles, such as the branched papillae of *Asteronotus raripilosa*, which are both variable (they tend to be lost in preserved specimens) and diagnostic (they are only found in *raripilosa*).

On the dorsal notum, one can also observe the rhinophores, the rhinophoral sheath, the gills, and the gill opening. Some authors have used the shape of the margins of the gill opening (as crenulate *vs.* smooth) and the shape of the rhinophoral sheath (as crenulate *vs.* smooth) to distinguish species. The examination of multiple specimens clearly demonstrates that this feature varies a great deal among individuals and should not be used to separate species. It is worth pointing out that the margin of the gill opening of *Platydoris* species is lobed (sometimes called 'star-shaped'), which cannot be confused with any form of crenulation. In most cases, animals have six branchial plumes. However, this number may vary among individuals for all sorts of reasons. Quite a few individuals have five or four branchial plumes, instead of six. Also, some species have more than six branchial plumes, such as *Discodorididae greeleyi*, which can have from eight to fourteen plumes. Branchial plumes can be more or less ramified. Most animals have multipinnate plumes, i.e., tripinnate or tetrapinnate. Exceptionally, branchial plumes can be unipinnate, such as in *Discodorididae greeleyi*. However, it seems that specimens with unipinnate branchial plumes are not part of the same species as specimens with tetrapinnate plumes. Finally, the number of rhinophoral lamellae, which has been used to distinguish species, also needs to be commented on. In all discodorid species for which a large number of specimens were available, the number of lamellae would vary a great deal among individuals. This character can hardly be used to distinguish species, especially because the numbers of lamellae found in different species often overlap: for example, there are from 22 to 40 lamellae in *Discodoris cebuensis*, 10 to 30 in *Sebadoris fragilis*, 10 to 30 in *Tayuva lilacina*, and 25 to 35 in *Sebadoris nubilosa*.

Some of the synapomorphies of discodorids are found on their ventral surface: a bilabiate anterior foot with a notched upper lip is found in all specimens; no exception was found. Of course, the depth of the notch of the upper lip may vary among individuals, but this might just be due to preservation. Also, all the discodorids examined had two oral tentacles, on either side of the mouth. Generally speaking, those tentacles are digitiform, although they can also be more conical in some individuals, probably depending on fixation and preservation. Whether the oral tentacles are digitiform or conical should certainly not be used to separate species. Some features, however, may not vary among individuals: some oral tentacles are distinctly flattened, such as in *Asteronotus raripilosa*; also, the oral tentacles of all *Paradoris* and *Platydoris* species are grooved longitudinally.

Digestive system

Traditionally, systematists have always assumed that the labial cuticle of individuals of a given species was either armed or smooth, but not both. For that reason, the presence *vs.* absence of jaw rodlets on the labial cuticle has been used by systematists to separate species. Also, species with an armed cuticle and species with a smooth cuticle have been placed in distinct genera: the most famous example certainly is the distinction between *Peltodoris* and *Discodoris*, exclusively based on the presence *versus* absence of jaws. The examination of hundreds of labial cuticle for the present study suggests that the presence/absence of jaws varies infra-specifically.

There are two species (*Discodorididae aurila*, *Discodorididae* sp. E) in which most specimens have a smooth labial cuticle, but a few specimens can bear a few isolated, distinct rodlets on each lateral side. Although complete jaws are absent in *aurila*, one cannot say that the labial cuticle of *aurila* is always smooth in all individuals. More commonly, there are quite a few species in which most specimens have an armed labial cuticle but a few specimens have a smooth labial cuticle. In the early stages of this study, it was thought that those labial cuticles were smooth because of a preparation artifact (e.g., labial cuticle put on the wrong side on the stub). But most labial cuticles are easily deposited on a SEM stub, and this mistake was certainly not repeated over and over. Therefore, at the end of this study, the idea that jaws can exceptionally be absent in species with an armed labial cuticle was accepted (e.g., *Discodoris boholiensis*, *Discodorididae coerulescens*, *Sebadoris fragilis*, *Tayuva lilacina*, *Sebadoris nubilosa*). Also, some species (e.g., *Discodoris boholiensis*, *Sebadoris nubilosa*) have a weakly-armed labial cuticle, in which case the labial cuticle might be hard to notice without SEM (e.g., *Asteronotus raripilosa*).

This has a major consequence on taxonomic practices. One should not assume that two specimens differing in the presence *vs.* absence of jaws are necessarily part of two distinct species. Eveline and Ernst Marcus have described twice the same species under two different names, *Peltodoris hummelincki* and *Tayuva ketos gila*, mainly because they overlooked the jaws in the specimen of *Peltodoris hummelincki* (here *Tayuva lilacina*) that they dissected.

Finally, the shape of the rodlet tips (pointed *vs.* rounded) cannot be used for distinguishing species because the shape of rodlet tips varies a great deal even within a single labial cuticle, mainly because they are continuously used to break food, and thus damaged (Dayrat 2006).

The radula provides powerful taxonomic characters. In fact, several clades are almost exclusively supported by radular features, such as *Geitodoris* and *Thordisa*. However, it is critical that we know about the infra-specific variation of all radular characters before we use them to distinguish species or for synapomorphies of clades. An important issue related to radular features is that workers rarely take the time to examine more than a few radulae (and often just more than one): so far, our knowledge of infra-specific variation has remained extremely limited, with few exceptions (Bertsch, 1976). The examination of a large number of radulae for several species provides us with the opportunity to comment on the infra-specific variation of several key features.

The first radular character that needs to be commented on is the shape of the radula. Three main radular shapes were recognized among the species studied. Most radulae are more or less square, or with a length that equals less than twice the width. *Paradoris* radulae are significantly elongated and narrow (Dayrat 2006). A third, distinct, radular shape was found in two species (*Hiatodoris fellowsi* and *Hiatodoris* sp. B): in these species, the two lateral sides of the radula are separated by a wide rachidian space, with a width that equals that of each lateral side; this wide rachidian space is free of teeth. Some variations were observed among individuals but those three radular shapes do not seem to overlap: every species has a radula of one type only.

Radular formulae have been mentioned in the literature for a long time, even in the early period when workers would not illustrate the teeth. However, few detailed studies have addressed the infra-specific variation of radular formulae: Bertsch (1976) analyzed the variation of radular formulae in *Discodorididae branneri* (as *Discodoris evelinae*) based on specimens of different sizes. In the present monograph, the variation of the radular formula is given for every species, based on present observations and the literature (misidentifications left aside). A vast number of radulae have been prepared in order to have a precise idea of infra-specific variation. Radular formulae vary a great deal infra-specifically depending on animal size. Some of the ranges observed are: from 14 to 56 rows and from 27 to 100 teeth per half row in *Sebadoris fragilis* (42 radulae prepared for this study); from 13 to 30 rows and from 13 to 40 teeth per half row in *Tayuva lilacina* (42 radulae prepared from specimens from the Indo-West Pacific); from 17 to 26 rows and from 35 to 56 teeth per half row in *Peltodoris atromaculata* (10 radulae prepared); from 12 to 24 rows and from 20 to 43 teeth per half rows in *Discodorididae aurila* (10 radulae prepared); from 10 to 42 rows and from 17 to 66 teeth per half rows in *Discodoris boholiensis* (12 radulae prepared); from 25 to 56 rows and from 55 to 130 teeth per half row in *Asteronotus raripilosa* (8 radulae prepared). The use of radular formulae to separate species is highly problematic unless one has dissected enough specimens to make sure that the ranges of variation do not overlap. Dissecting many specimens yields interesting information, however: for example, *Tayuva lilacina* never has more than 40 teeth per half row (at least in the tropical Indo-West Pacific), whereas only three radulae with less than 40 teeth per half row were found in *Sebadoris fragilis*, which means that one can potentially distinguish *Tayuva lilacina* and *Sebadoris fragilis* by combining the size of the animals and the radular formulae.

The shape of the radular teeth is, of course, of great taxonomic importance. Most teeth in discodorids are simply hamate. Some species, however, are characterized by hamate teeth that display interesting differences from the common type. The species that belong to *Discodoris sensu stricto* (*boholiensis*, *cebuensis*, and sp. A) have teeth with a significantly elongated hook; also, the tooth base bears a wing on its inner, dorsal edge, from the radular membrane up to the hook, which appears as a strong spur on the inner edge of the teeth; this spur is present in all individuals. In some other species (e.g. *Peltodoris atromaculata*, *Peltodoris murrea*), the ten or so innermost teeth are significantly smaller that the rest of the lateral teeth, which gives to the radula a distinct and easily recognizable appearance. In many cases, the outermost teeth are straight (instead of hamate). However, this varies a great deal within a single radula and among individuals. Several discodorid clades have peculiar, easily recognizable teeth, used to transfer several *Discodoris* species to those taxa, such as *Rostanga* (thin, elongated teeth) or *Geitodoris* (spatulate outermost teeth). Although the shape of those radular teeth is useful at supra-specific levels, it varies a great deal within each species: the case of *Rostanga crawfordi* is discussed in the present study; the infra-specific variation in *Geitodoris* radulae will be discussed in a revision published separately.

Some important features of the radular teeth are the denticles. There is a great diversity of denticles. They differ in shape, position, and size. Most denticles are found on the outer side of the hook, and in most cases (for the species studied here, not in all discodorids) in the last three to five outermost teeth. Some, however, are found on the inner side, such as in the first innermost lateral tooth of *Discodoris boholiensis* and *Discodoris cebuensis*, as well as some *Rostanga* species. When on the outer side of the hook, denticles can be apical, marginal (i.e., on the lateral edge), or just on the outer, flattened part of the hook. The type of denticles found in a given species does not vary infra-specifically: denticles are not on the inner side of the hook in some individuals and on the outer side of the hook in some other specimens (unless a species has both outer *and* inner denticles). However, the size and number of denticles vary a great deal among individuals. Most species whose radular teeth have denticles also include individuals with smooth radular teeth. Reciprocally, species were found with smooth outermost teeth that exceptionally bear one or a few denticles (e.g., *Discodorididae coerulescens*, *Tayuva lilacina*). More importantly, the size and number vary a great deal within a single radula. However, there are many species in which denticles were never observed, even after dissecting dozens of radulae, such as in *Discodorididae branneri* and *Sebadoris fragilis*. Interesting cases of infra-specific variation of denticles of the outermost teeth are found in *Discodorididae aurila*, *Discodorididae coerulescens*, *Discodorididae mortenseni*, *Discodorididae muta*, and *Discodorididae* sp. D. The presence *vs.* absence of denticles should only be used with great caution: one should only use it to distinguish species only after many specimens have been dissected.

Jaws and radulae are not the only organs found in the digestive system. Other interesting features are: the position of the stomach, the size of the caecum (stomach), and the length and shape of the intestine. In most species, the stomach is large, free on top of the left dorsal side of the digestive gland, a small caecum is found on the posterior side of the stomach, and the intestine is dorsal (i.e, on the dorsal side of the digestive gland) and straight. In some other species (e.g., *Discodoris boholiensis*, *Discodorididae flindersi*), the stomach is narrow, on top of the median, dorsal side of the digestive gland. In some species (e.g., *Peltodoris fellowsi*), the stomach can be large and free or narrow and median. The position of the stomach may not have any supra-specific significance because *Discodoris cebuensis*, which is obviously closely related to *Discodoris boholiensis*, has a stomach that is large, free on top of the left dorsal side of the digestive gland. In any case, it can hardly be used at supra-specific levels because it varies infra-specifically.

In some species, the intestine is not straight: for example, in *Discodorididae branneri*, some individuals (not all) have a long intestine with a loop on the right lateral side of the digestive gland; in *Sebadoris fragilis*, all adult specimens have a long, intestine, with a long loop either on the right lateral side of the digestive gland, or (in most cases) underneath the digestive gland (a straight intestine may be found in some young specimens). In all specimens of *Sebadoris nubilosa* dissected, the intestine was very long and highly convoluted (with several loops) from the stomach up to the anus.

Finally, most species have a small caecum, but large caeca can also be found. In *Sebadoris fragilis*, most specimens have a large caecum, and only a few have a regular, small caecum (which is not correlated to animal size); a large caecum was also found in the *Sebadoris nubilosa* specimens dissected, but fewer specimens of *nubilosa* than *fragilis* were dissected (so one could expect to find a small caecum in other *nubilosa* individuals). It seems that somehow the size of the caecum and the length of the intestine are correlated (large caeca and long intestine are both found in *fragilis* and *nubilosa*).

Nervous system

In brief, the nervous system is taxonomically useless at specific and supra-specific levels in discodorids. It would seem to be impossible to identify or distinguish species based on their nervous system. In theory, one would expect to find identical nerves in all individuals of one given species (and probably in closely related species as well), but in practice one usually finds different nerves because of preservation (fragile nerves break easily). Also, it is unclear that dissection is the most appropriate way to study the anatomy of the nervous system. One would probably need to use histology. In any case, it is unlikely that the nervous system will provide strong characters that could be used in discodorid alpha-taxonomy. The length of the circum-esophageal nerve ring, which varies in nearly all species, cannot be used to distinguish species.

Reproductive system

The reproductive system provides some of the most powerful features for species identification. In particular, the general organization of the reproductive system is useful. By 'general organization,' it is referred to the relative positions of the different structures: ampulla, female gland mass, prostate, deferent duct, penial sheath, accessory glands, vaginal duct, bursa copulatrix, fertilization duct, and receptaculum seminis. It seems that each species has a reproductive system with a diagnostic organization. Unfortunately, this diagnostic organization varies among individuals and may be affected by fixation and preservation, as well as by the age and size of animals. It is commonly found that reproductive systems are immature. An efficient way to determine whether a reproductive system is immature or not is the size of the female gland mass: adult, sexually mature animals have a large, fully developed female gland mass (likely because discodorids are protandric).

It is nearly impossible to describe the organization of a reproductive system with words: two reproductive systems described with similar words could be identical or totally different. For example, the description of a "loosely convoluted deferent duct" could apply to many species. It is not the fact that a deferent duct is loosely convoluted which is important, but *how* it is convoluted. Therefore, the organization of a reproductive system is best represented by a drawing. However, only drawings that represent *exactly* the reality are informative. Drawings that are schematic or that do not represent exactly the actual arrangement seen under the scope are less informative because they do not represent the most important components of a reproductive system, i.e., the fine details that are useful taxonomically. Examples of reproductive systems with a strikingly diagnostic organization are found in *Discodorididae aurila*, *Discodorididae coerulescens*, *Sebadoris fragilis*, *Discodorididae mortenseni*, and *Peltodoris murrea*. Features from the reproductive system are commented below, with an emphasis on their infra-specific variation.

The male and female gametes are produced in the hermaphroditic gland (also called ovotestis). The latter is mixed with the digestive gland in nearly all species; the hermaphroditic and digestive glands cannot be separated without destroying the tissues, although they can be distinguished because they usually differ in color and texture. Exceptionally, however, the hermaphroditic gland is independent of the digestive gland and can be easily separated from it. Of all the species redescribed here, only one, *Discodorididae coerulescens*, has an independent hermaphroditic gland. However, an independent hermaphroditic gland is also present in the type material of *Alloiodoris marmorata* Bergh, 1904 (re-examined but not included in this monograph). Whether the hermaphroditic gland is independent from or mixed with the digestive gland does not vary infra-specifically: all *marmorata* and *coerulescens* specimens examined have an independent hermaphroditic gland.

The length of the ampulla is highly variable infra-specifically. Many species were found in which the ampulla could be convoluted from one up to many times. The number of loops of the ampulla should probably not be used to identify or distinguish species. At some point, the ampulla divides in two (female and male) ducts. This branching is often drawn by systematists. However, it was observed only a few times in the context of this work. This branching, which is embedded within the female gland mass, is indeed difficult to see, and it is likely that people draw it just because they know that it is there.

The male duct runs through the prostate before it becomes the deferent duct, which ends into the genital openings (with or without male copulatory organ). In discodorids, the prostate is flattened and divided in a distal part and a proximal part (which can be distinguished with their color) in nearly all cases. There are some exceptions, however: a few species have a tubular prostate, such as *Discodorididae achroma* and *Paradoris dubia*. Also, a few species have a prostate that is divided in three parts (each with a different color), such as *Sebadoris fragilis*, and *Tayuva lilacina* (in which most individuals have a prostate divided in three parts, but some individuals have a prostate only divided in two parts).

The shape, the length, and the loops of the deferent duct can be diagnostic and useful in taxonomy. However, the deferent duct presents a great deal of infra-specific variation, so a large number of individuals should be dissected before the arrangement of the deferent duct can be considered to be diagnostic of a particular species. The deferent duct is narrow in nearly all species. *Tayuva* has a distinct deferent duct: in its proximal part, it is enlarged and folded internally (although a few individuals only have a narrow deferent duct). The number of loops of a deferent duct is correlated to its length. A very long deferent duct tends to be highly convoluted, whereas a short deferent duct tends to be straight or loosely convoluted. However, the length and number of loops vary a great deal infra-specifically, mainly depending on the age of animals and whether or not they are sexually mature. Some species (e.g., *Discodoris boholiensis*) have fully mature reproductive systems (recognized by the large size of the female gland mass) with a long, highly convoluted deferent ducts, and young, immature systems with a shorter, loosely convoluted deferent duct. In some other species (e.g., *Discodorididae cebuensis*), a similar variation was not correlated to the age or maturity of the animals. The opposite situation was also encountered in which fully mature individuals have a short deferent duct and not fully mature individuals a long deferent duct (e.g., *Discodorididae mortenseni*). It is worth pointing out that the length and number of loops of the deferent duct does not vary in all species. Indeed, in a few species (e.g., *Sebadoris fragilis* and *Tayuva lilacina*), all individuals have either a straight, short deferent duct or a long, convoluted deferent duct. More important than the number of loops is their position with respect to other structures. Indeed, in some species (e.g., *Discodorididae mortenseni*, *Peltodoris murrea*), it is possible to identify a specific, diagnostic arrangement of the deferent duct.

The deferent duct ends into the male genital opening. Some species have no distinct copulatory organs, which means that the distal part of the deferent duct simply evaginates to transport sperm cells to the outside or to the partner. In some cases, however, the deferent duct ends into a distinct, permanent, copulatory organ protected into a penial sheath. Distinguishing between evaginable deferent duct and copulatory organ is easy when the penis is large or armed with spines. In species (e.g., *Discodorididae mortenseni*) where the penis is just a small penial papilla, it can be more difficult to decide. However, I think that a penis should be found in all individuals, whereas a papilla that is just the evaginated, distal part of the deferent duct will not be found in all individuals.

The shape of the penis probably is one of the most important taxonomic features, which likely is due to the fact that, being sexual organisms, distinct copulatory organs lead to reproductive isolation, and, reciprocally, reproductive isolation leads to distinct copulatory organs. Because of the importance of penial morphology in taxonomy, it is critical that workers always illustrate copulatory organs, regardless of whether they are armed with spines or not (because even the shape of an unarmed penis is critical in taxonomy). Ideally, penial morphology should be illustrated with SEM pictures, because it gives access to details that otherwise are overlooked. Penial morphology can be used to identify species even though it varies a great deal infra-specifically. Several good examples of this are: *Discodorididae branneri*, characterized by a penis covered with strong conical spines; *Sebadoris nubilosa*, characterized by a coiled penis bearing two longitudinal rows of humps, although some young individuals have a smooth, uncoiled penis; *Discodorididae rubra*, characterized by a large penis bearing conical papillae of which the size, position, and number vary among individuals. In some cases, species may share a similar penial shape (e.g., *Tayuva*), although this could be due to the fact that there is only one species with a worldwide distribution. One species was found (*Discodorididae coerulescens*) where the penis morphology varies much more than expected (penis absent or present, and with or without small papillae): it is unclear whether this is a case of exceptionally high infra-specific variation, or if it is simply due to the fact that *Discodorididae coerulescens* is a species complex with several cryptic units. Finally, penis size tends to be more or less consistent among individuals: for instance, most of the individuals of *Tayuva lilacina* dissected had a penis that measured less than 1 mm. However, when discussing the penis length, one also needs to take into account the shape: for example, the penis of *Sebadoris fragilis* ranges from 0.1 up to 1.3 mm in length, but the long penises are narrow (and elongated) whereas the short penises are conical.

Another interesting structure is the distal muscular wall. When present, the latter surrounds the penial sheath or the entire distal region of the reproductive system. This muscular wall was only found in *Tayuva*, in nearly all individuals of *lilacina*. The shape and size of the muscular wall vary infra-specifically.

The exosperm is transported in the vaginal duct and then is stored in two spermatic pouches: the receptaculum seminis (called also 'spermatocyst') and the bursa copulatrix (called also 'spermatheca'). The length and the shape of the vaginal duct vary among individuals, but within a much more restricted range than for the deferent duct. Within a given species, the vaginal duct can be straight and loosely convoluted, but it is not straight and highly convoluted. Also, generally speaking, the vaginal duct is less convoluted than the deferent duct, probably because there is no real advantage in having a long vaginal duct since the main function of the vaginal duct is to transport exosperm cells to the bursa. In most discodorid species, two ducts open into the bursa: the vaginal duct, and the fertilization duct (also called uterine duct) that goes from the bursa to the fertilization chamber (embedded within the female gland mass). However, in a few, exceptional species (e.g., *Discodorididae achroma*, *Paradoris dubia*), only one duct (the vaginal duct) reaches the bursa, and the fertilization duct connects the vaginal duct to the fertilization chamber, instead of connecting the bursa copulatrix to the fertilization chamber. In any case, the length of the fertilization duct varies infra-specifically, but within a much more restricted range than for the deferent duct. More importantly, in some species, the fertilization duct is arranged in a conspicuous, specific, diagnostic way. One of the best examples is found in *Sebadoris fragilis*, whose fertilization duct was positioned exactly in the same recognizable way in all specimens (with a U-shaped loop on the surface of the bursa); another example is found in *Discodorididae aurila*, whose fertilization duct also displays a peculiar arrangement.

In most species in which many specimens could be dissected, it was found that the relative size of the spermatic pouches varies a great deal among individuals: in *Peltodoris atromaculata*, the bursa copulatrix is from two to ten times larger than the receptaculum seminis; in *Tayuva lilacina* (Mediterranean and eastern Atlantic) the bursa is from two to ten times larger than the receptaculum; in *Tayuva lilacina* (Caribbean), the bursa is from one to seven times larger than the receptaculum; in *Sebadoris nubilosa*, the bursa is from one to seven times larger than the receptaculum. However, in a few species, no variation was noticed (e.g., *Discodoris boholiensis*, *Discodoris cebuensis*), which certainly does not mean that there is no variation (looking at more specimens would certainly yield some variation).

The shape of the bursa varies (infra-specifically) from spherical to ovate, although it is spherical-ovate in most specimens. The shape of the receptaculum seminis tends to be more variable: it can be elongated or spherical-ovate. The range of infra-specific variation of the shape of the receptaculum depends on the species considered: for example, the receptaculum of *Discodorididae branneri* is elongated in most cases, but exceptionally spherical-ovate, whereas in *Tayuva lilacina* (at least in eastern Pacific) it is both spherical-ovate and elongated. It is suspected, however, that the observation of more specimens would ultimately yield some variation. Also, with the shape and size of spermatic pouches (as with most 'soft' features), it is uncertain whether the variation observed is natural or an artifact due to fixation and preservation. Finally, the length of the duct of the receptaculum seminis (which goes from the fertilization duct up to the receptaculum) is short in most species, except in some cases (e.g., *Paradoris erythraeensis*) where it is significantly longer than usual.

Accessory vestibular glands are commonly found in discodorids. However, their homology is poorly known. There are accessory glands that are clearly distinct, such as the 'stylet sacs' found in some *Paradoris* species (Dayrat 2006) and the stylet sacs found in *Jorunna* (Camacho-García and Gosliner 2008). Although those structures are all called stylet sacs, they are anatomically distinct. Now, there are other cases where distinguishing accessory glands (i.e., determining their primary homology) is less obvious. This is specifically true for all the accessory vestibular glands with a hollow spine, such as the ones found in *Asteronotus* and *Carminodoris*. As far as this study is concerned, however, species traditionally classified within *Discodoris*, *Peltodoris*, and *Anisodoris* species had no vestibular glands, which explain why vestibular glands were found only in species that were clearly misplaced, such as *Paradoris indecora* and *Asteronotus raripilosa*. However, the shape of the spine of accessory gland of *Asteronotus raripilosa* presents an interesting individual variation: the conical spine of adult, fully mature individuals is curved, whereas it is straight in younger individuals, which means that the shape of the spine of the accessory gland can be used for distinguishing species only if individual variation is addressed.

Finally, the size of the glands of the female gland mass (albumen and mucous glands) varies a great deal infra-specifically. Discodorids seem to be protandrous, which means that the female parts tend to mature and develop after the male parts. Many individuals with fully developed male parts and a reduced female gland mass were found. No feature in the female gland mass was found to be taxonomically informative, except in one case: when sexually mature, the female gland mass of *Peltodoris murrea* is much larger than in all other species examined and covers the entire reproductive system.

Diversity and Synonymy

The taxonomic revision of *Discodoris*, *Peltodoris*, and *Anisodoris* species required considering a total of 119 species names and 6 subspecific names. The Appendix 1 indicates the former and current status of all those names.

Prior to the present study, the status of those 125 names included: 106 valid names, 13 synonyms, two *nomina dubia*, three permanently invalid names, and one *nomen nudum*. After the present revision, the status of the same names includes: 39 valid names, 12 synonyms (out of the 13 former synonyms), 25 new synonyms, 27 *nomina dubia*, three permanently invalid name, one *nomen nudum*, and 18 names of poorly-known species. These names of poorly-known species could be *nomina dubia*, synonyms, or valid names. In most cases, names that refer to "poorly-known species" should probably be regarded as *nomina dubia*. However, whenever there was any hope that one could find new specimens, those names were not regarded as *nomina dubia*: names are regarded here as *nomina dubia* in a very conservative way. However, the names that refer to poorly-known species are names that currently are dubious (because their exact application is currently unknown), although this situation might change when more material becomes available.

Cladistic Analyses

Topology and clade support

The cladistic analysis with only the valid species (analysis #1) yielded a strict consensus tree (59 steps) with some resolution (Fig. 2). The general topology of that tree is globally similar to that found in previous analyses (Dayrat and Gosliner 2005; Dayrat 2005a), with a few interesting modifications though.

The monophyly of *Discodorididae* is confirmed here again (Bremer support value of 2), which is not surprising given that identical characters were used. The synapomorphies of *Discodorididae* are: notched upper lip of the bilabiate anterior foot; digitiform oral tentacles; flattened prostate divided in two (proximal and distal) parts; two blood glands. *Discodorididae* include a large, metaphyletic group of 21 basal species and 13 subclades. The latter can hardly be subdivided, except for one of them (Bremer support value of 1), which includes *Geitodoris* (Bremer support value of 1) and *Paradoris* (Bremer support value of 6).

The caryophyllidia-bearing dorids are not grouped into a monopyletic taxon, because the only character that could be a synapomorphy (presence of caryophyllidia) is contradicted by several other characters. As a consequence, the species in the metaphyletic group at the base of *Discodorididae* are both caryophyllidia-bearing dorids (*aurila*, *greeleyi*, *lancei*, *lippa*, *punctuolata*, *sandiegensis*, sp. D, and sp. E) and species with a dorsal notum that does not bear caryophyllidia (*achroma*, *aliciae*, *branneri*, *coerulescens*, *labifera*, *lentiginosa*, *nobilis*, *rubra*, *worki*, sp. C, sp. F, and sp. G). Note that it is still unclear whether *mortenseni* bears caryophyllidia or not.

Two new and interesting subclades of *Discodorididae* are: (*atromaculata*, *mullineri*, *murrea*) and (*boholiensis*, *cebuensis*, sp. A). Indeed, *atromaculata* is the type species of *Peltodoris*, and *boholiensis* is the type species of *Discodoris*. Therefore, both genera, which have been problematic for decades, can now apply to distinct, well-delineated clades.

The monophyly of *Peltodoris* (Bremer support value of 1) is supported by the presence, in the radula, of about 10 to 15 innermost teeth that are significantly smaller than the rest of the lateral teeth. Their size and arrangement (they tend to lay on the radular membrane instead of being erect) can hardly be confused. Also, a radula of *atromaculata* could probably not be distinguished from a radula of *murrea* or *mullineri*.

The monophyly of *Discodoris* (Bremer support value of 1) is also supported by a radular feature: indeed, the hook of the hamate teeth of *boholiensis* and *cebuensis* could not be distinguished and are different from other discodorids; the shape of the teeth of sp. A differs a little bit but share with those two species the peculiar, long and narrow tooth hooks.

The clade that includes *fellowsi* and sp. B, two caryophyllidia-bearing species, is new (Bremer support value of 1). Again, those two species have a similar radula, which also is distinct from other discodorids: it is characterized by a large, empty rachidian space in between the two lateral sides of the radula. A new name is created for this clade (see below).

The clade that includes *fragilis* and *nubilosa* is also new (Bremer support value of 1). Interestingly, those two species have been often confused, based are the dorsal color, although their internal anatomy (especially the penial morphology) is different. However, they share two peculiar features in the digestive system: a very long, convoluted intestine, and a significantly larger caecum. Given that *nubilosa* is the type species of *Sebadoris*, this clade can be called *Sebadoris*.

Doris raripilosa, a species that was classified in six different genera (if one considers synonyms and misidentifications), can be positively classified within *Asteronotus* (Bremer support value of 1). Indeed, *raripilosa* and *cespitosus* (the type species of *Asteronotus*) share a peculiar shape of the base of the radular teeth (convex instead of concave), which is especially striking in the innermost teeth. They also share other features such as flattened oral tentacles (which could be just due to their large size), and the presence of a vaginal accessory gland with a hollow spine, although other discodorids also share similar accessory glands (e.g., *Carminodoris* species).

Discodoris crawfordi is transferred to *Rostanga* (Bremer support value of 1). As expected, *Geitodoris* and *Paradoris* are monophyletic. The other clades, introduced in the analyses for the sake of the general topology of the tree, are similar to previous analyses (Dayrat and Gosliner 2005): *Carminodoris* (*grandiflora* and *estrelyado*, Bremer support value of 2), *Jorunna* (*pardus* and *tomentosa*, Bremer support value of 1), *Platydoris* (*argo* and *ellioti*, Bremer support value of 4), *Aporodoris* (*aivica* and *fanabensis*, Bremer support value of 1), and *Thordisa* (*bimaculata* and *filix*, Bremer support value of 1); *Tayuva lilacina* refers here to a widely distributed species or group of species. The name *Tayuva* is kept for it, although *Tayuva*, at present, is monotypic, because it is likely that *Tayuva lilacina* is a species complex, with potential cryptic species in the Indo-West Pacific.

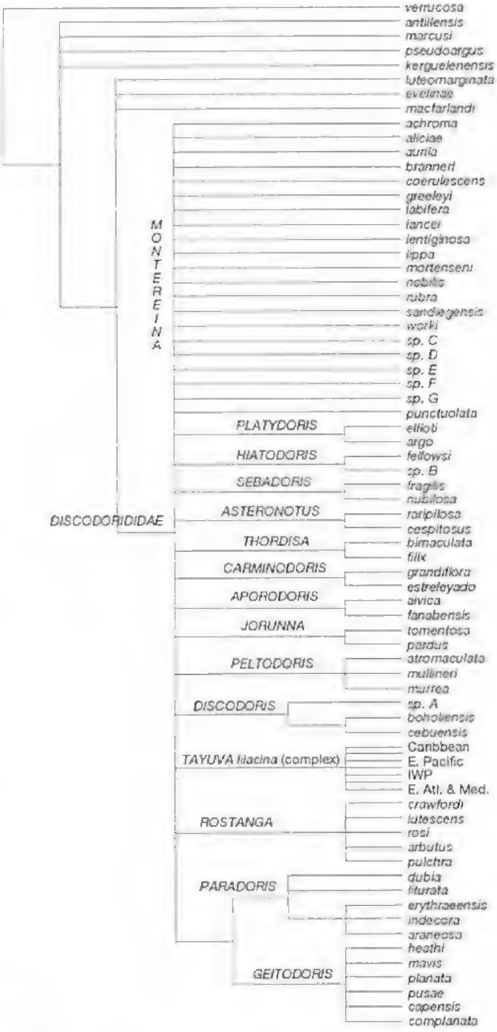

FIGURE 2. Phylogenetic relationships among discodorid species (analysis #1, see text). The taxon name "*Montereina*" can be used under the *ICZN* as a generic name for all the species that belong to the metaphyletic group at the base of *Discodorididae*. Otherwise, in the context of the *ICPN*, the clade name *Discodorididae* can be placed in front of the specific names of all species that belong to that metaphyletic group, e.g., *Discodorididae branneri*.

Phylogenetic position of *nomina dubia* and poorly known species

The phylogenetic position of *nomina dubia* and poorly known species was addressed separately, i.e., once the relationships among valid species were addressed, so that the question marks that *nomina dubia* and poorly known species introduce in the data matrix would not interfere with the phylogenetic reconstruction among valid species. Below are summarized all the results of the additional analyses #2 to #20. Only the topology of the strict consensus tree is mentioned. In all analyses, the number of steps was 59, except in analyses #2, #3, #7bis and #21 (60 steps), and #7b (61 steps). Because consensus trees from those analyses #2 to #20 displayed little resolution or were very similar to analysis #1 (Fig. 2), their topology is simply described in words below.

Analysis #2. All valid species, all *nomina dubia*, and all poorly known species.— Topology: no resolution at all.

Analysis #3. All valid species, no *nomina dubia*, all poorly known species except for *edwardsi*, *rubescens*, and *stellifera*.— Topology: seven clades (*Discodorididae*, *Aporodoris*, *Carminodoris*, *Geitodoris*, *Paradoris*, *Platydoris*, and *Thordisa*); all poorly known species sampled are part of the metaphyletic group at the base of *Discodorididae*, except for *prea* that does not belong to *Discodorididae*.

Analyses #4. All valid species, no *nomina dubia*, no poorly known species except for *edwardsi*.— Topology: same as in Analysis #1 (Fig. 2), except that *Discodorididae* now includes three of the out-groups (*luteomarginata*, *evelinae*, and *macfarlandi*) as well as *edwardsi*.

Analyses #5. All valid species, no *nomina dubia*, no poorly known species except for *rubescens*.— Topology: eight clades (*Carminodoris*, *Discodoris*, *Geitodoris*, *Paradoris*, (*Geitodoris* + *Paradoris*), *Platydoris*, *Aporodoris*, *Tayuva*); *Discodorididae* not monophyletic; *rubescens* may or may not be part of *Discodorididae*.

Analyses #6. All valid species, no *nomina dubia*, no poorly known species except for *stellifera*.— Topology: one clade only (*Platydoris*); *Discodorididae* not monophyletic; *stellifera* may or may not be part of *Discodorididae*.

Analysis #7. All valid species, all *nomina dubia* (except for *angulata*, *granulata*, *maculosa* Cuv., *noumeae*, *patriziae*, *schmeltziana*, *sordii*, *testudinaria*, *timorensis*, and *versicolor*), and no poorly known species.— Topology: three clades (*Discodorididae*, *Carminodoris*, and *Platydoris*); all *nomina dubia* sampled are part of the metaphyletic group at the base of *Discodorididae*.

Analysis #7bis. All valid species, all *nomina dubia* (except for *angulata*, *granulata*, *maculosa* Cuv., *noumeae*, *patriziae*, *schmeltziana*, *sordii*, *testudinaria*, *timorensis*), and all poorly known species (except for *edwardsi*, *rubescens*, and *stellifera*).— Topology: three clades (*Discodorididae*, *Carminodoris*, and *Platydoris*); all *nomina dubia* and poorly known species sampled are part of the metaphyletic group at the base of *Discodorididae* (except for *versicolor* and *prea*, which do not belong to *Discodorididae* and are with the outgroups).

Analyses #8 to #12, #14, and #15. All valid species, no *nomina dubia* except for *angulata* (#8), *maculosa* Cuv. (#9), *noumeae* (#10), *patriziae* (#11), *schmeltziana* (#12), *testudinaria* (#14), and *timorensis* (#15), and no poorly known species.— Topology: a few clades depending on the analysis (e.g., only *Asteronotus* and *Platydoris* in Analysis #9); *Discodorididae* never monophyletic; *angulata*, *maculosa* Cuv., *noumeae*, *patriziae*, *schmeltziana*, *testudinaria*, and *timorensis* may or may not be part of *Discodorididae*.

Analysis #13. All valid species, no *nomina dubia* except for *sordii*, and no poorly known species.— Topology: ten clades (*Discodorididae*, *Asteronotus*, *Carminodoris*, *Discodoris*, *Geitodoris*, *Paradoris*, (*Geitodoris* + *Paradoris*), *Platydoris*, *Rostanga*, *Tayuva*); *sordii* belongs to *Discodorididae*.

Analysis #16. All valid species, no *nomina dubia* except for *versicolor*, and no poorly known species.— Topology: same as in Analysis #1 (Fig. 2), with *versicolor* that does not belong to *Discodorididae* (nested with outgroups).

Analysis #17. All valid species, no *nomina dubia*, and no poorly known species (except for *millegrana*).— Topology: same as in Analysis #1 (Fig. 2), with *millegrana* nested with two *Taringa* species (*aivica* and *fanabensis*). There are two possible genus names for that clade: *Aporodoris* von Ihering, 1886, type species *millegrana*, and *Taringa* Marcus, 1955. However, *Aporodoris* has priority over *Taringa* because *ICZN* Article 23.9 does not apply here (see *Aporodoris millegrana* for more discussion).

Analysis #18. All valid species, no *nomina dubia* (except for *rubens*), and no poorly known species.— Topology: same as in Analysis #1 (Fig. 2), with *rubens* nested with *Geitodoris* species.

Analysis #19. All valid species, no *nomina dubia* (except for *tristis*), and no poorly known species.— Topology: same as in Analysis #1 (Fig. 2), with *tristis* as sister-taxon of *Paradoris*.

Analysis #20. All valid species, no *nomina dubia* (except for *tristis*), and no poorly known species (and one coding change: character #8 changed for *tristis* from absence or presence to presence of lobes of the branchial sheath).— Topology: same as in Analysis #1 (Fig. 2), except that *Platydoris* is not monophyletic.

In summary, all *nomina dubia* and poorly known species for which characters #1 and #2 are known (and apomorphic) belong to *Discodorididae*. Also, *sordii* (*nomen dubium*), a species for which the coding of characters #1 and #2 was uncertain, also belongs to *Discodorididae*. Other positive positions are that of *versicolor* and *prea*, which do not belong to *Discodorididae*. Within *Dis-*

codorididae, *rubens* (*nomen dubium*) belongs to *Geitodoris*, which is clearly due to the presence of outermost pectinate teeth in its radula (a synapomorphy of *Geitodoris*), and *millegrana* belongs to *Aporodoris*, due to the presence of a penial cuticle and outer denticles on the tooth hooks. All other *nomina dubia* (*angulata*, *maculosa* Cuv., *noumeae*, *patriziae*, *schmeltziana*, *testudinaria*, and *timorensis*) and poorly known species (*edwardsi*, *rubescens*, and *stellifera*) may or may not belong to *Discodorididae*.

Metaphyly at the base of *Discodorididae*

A total of 50 species are part of the metaphyletic group at the base of *Discodorididae*. This includes: 21 valid species (*achroma*, *aliciae*, *aurila*, *branneri*, *coerulescens*, *greeleyi*, *labifera*, *lancei*, *lentiginosa*, *lippa*, *mortenseni*, *nobilis*, *punctuolata*, *rubra*, *sandiegensis*, *worki*, sp. C, sp. D, sp. E, sp. F, and sp. G); 17 *nomina dubia* (*alba*, *amboinensis*, *caerulescens variegata*, *concinna*, *concinniformis*, *crucis*, *hummelincki igla*, *modesta*, *muta*, *notha*, *opisthidia*, *pardalis*, *sordii*, *tristis*, *voniheringi*, *yaeyamensis*, and *zibethina*); and 12 poorly-known species (*aurea*, *erubescens*, *flindersi*, *golaia*, *pallida*, *paroa*, *phoca*, *punctifera*, *purcina*, *sauvagei*, *A. sibogae*, and *ylva*).

It is worth listing the nine genera in which all those species have been classified (synonyms and misidentifications not considered): *Anisodoris* (*flindersi*, *lentiginosa*, *nobilis*, *punctuolata*, *sibogae*, *worki*), *Archidoris* (*nobilis*), *Carminodoris* (*branneri*), *Diaulula* (*aurila*, *greeleyi*, *punctuolata*, *sandiegensis*), *Discodoris* (*achroma*, *alba*, *aliciae*, *amboinensis*, *aurila*, *branneri*, *caerulescens variegata*, *coerulescens*, *concinna*, *concinniformis*, *crucis*, *erubescens*, *golaia*, *labifera*, *modesta*, *mortenseni*, *muta*, *notha*, *opisthidia*, *pardalis*, *paroa*, *phoca*, *purcina*, *rubra*, *sandiegensis*, *sauvagei*, *sordii*, *tristis*, *voniheringi*, *yaeyamensis*, *ylva*, *zibethina*), *Doris* (*concinna*, *crucis*, *labifera*, *pardalis*, *punctifera*, *punctuolata*, *sandiegensis*), *Fracassa* (*zibethina*), *Montereina* (*nobilis*), and *Peltodoris* (*aurea*, *crucis*, *greeleyi*, *hummelincki igla*, *nobilis*, *lancei*, *lentiginosa*, *lippa*, *punctifera*, *sauvagei*, *sordii*).

Once obvious mistakes (*Carminodoris branneri*, *Archidoris nobilis*), monotypic genera (*Fracassa zibethina*, *Montereina nobilis*), and *Doris* historical artifacts (*Doris* was used as a genus name in the early days when no other genera were available) are removed, then only four genera remain in this list: *Anisodoris*, *Diaulula*, *Discodoris*, and *Peltodoris*.

It also is worth mentioning here that three of all those species are type species: *punctuolata* for *Anisodoris*; *sandiegensis* for *Diaulula*; and *zibethina* for *Fracassa*.

Classification

Based on the phylogenetic relationships described above, one can construct the following classification within *Discodorididae*:

A large metaphyletic group at the base of *Discodorididae* includes 50 species (i.e., 21 valid species, 17 *nomina dubia*, and 12 poorly known species; see above).
Then a series of discodorid sub-clades, all ranked at the generic level under the *ICZN*, are well supported:
Discodoris (including the two valid species *boholiensis* and *cebuensis*, and a new, unnamed species).
Peltodoris (including the three valid species *atromaculata*, *mullineri*, and *murrea*).
Tayuva (including at present only one widely-distributed species, *lilacina*, but that likely will be split in more than one entity when non-morphological data are available).
Sebadoris (including the two valid species *nubilosa* and *fragilis*).
Asteronotus (including the two valid species *cespitosus* and *raripilosa*, as well as one or two valid species not sampled here; see, Gosliner and Valdés 2002)
Paradoris (for more information, see: Dayrat 2006; Camacho-García and Gosliner 2007).

Geitodoris (the exact number of species is uncertain at this stage; a manuscript of a revision is in preparation). *Geitodoris* and *Paradoris* may be sister-taxa.
Hiatodoris (a new taxon name, including *fellowsi* and a new, unnamed species).

To these clades, must be added other taxa introduced in the analyses in order to have a more representative taxon sample but not revised here: *Aporodoris* (=*Taringa*), *Carminodoris*, *Jorunna* (Camacho-García and Gosliner 2008), *Platydoris* (Dorgan et al. 2002), *Rostanga* (to which a few *Discodoris* species are transferred here; see, also, Avern and Rudman 1989; Garovoy et al. 2001), and *Thordisa* (Chan and Gosliner, 2007).

Not all discodorid taxa are represented here: several generic taxa such as *Halgerda* (e.g., Fahey and Gosliner 2000), *Baptodoris*, and *Atagema* (e.g., Valdés and Gosliner 2001) are missing. Again, the main goal of the present revision was to deal with all *Discodoris* and *Peltodoris* species names.

Species Binomials

New combinations

Based on the phylogenetic relationships described above, some species can be re-allocated. Some species are not problematic because they can be transferred to a clade that can be ranked at the genus level (*ICZN*). Within the species descriptions, for each species, all previous combinations proposed so far are mentioned, as well as the new combination proposed here.

Doris fragilis and *Discodoris fragilis* should become *Sebadoris fragilis*. *Doris raripilosa* and *Discodoris raripilosa* should become *Asteronotus raripilosa*. *Doris murrea* and *Platydoris murrea* should become *Peltodoris murrea*. *Discodoris crawfordi* should become *Rostanga crawfordi*. *Discodoris rubens* (*nomen dubium*) should become *Geitodoris rubens*. *Taringa aivica* and *Taringa fanabensis* should become *Aporodoris aivica* and *Aporodoris fanabensis*, for nomenclatural (not taxonomic) reasons (same re-allocation applies to all *Taringa* species that belong to that clade). Note that all synonyms are indirectly also re-allocated to new genera: e.g., *Alloiodoris hedleyi* should become *Sebadoris hedleyi*, junior synonym of *Sebadoris fragilis*.

Problematic binomials

The fact that 50 species cannot be placed in any of the discodorid subclades leads to a problematic nomenclatural situation: in our phylogenetic analyses (see above), those species are placed in the metaphyletic group at the bases of *Discodorididae*, so we know that those species belong to the clade *Discodorididae*, but we cannot place any of them in any of the discodorid subclades regarded traditionally as generic taxa (e.g., *Platydoris*, *Geitodoris*, etc.). *Discodoris* and *Peltodoris* now refer to well-defined clades (Fig. 2), and cannot be used as a generic name for species other than the ones that belong to those clades, and certainly not for the species that belong to the metaphyletic group at the base of Discodorididae.

As a consequence, there are 29 *Discodoris* species (*achroma, alba, aliciae, amboinensis, branneri, caerulescens variegata, coerulescens, concinna, concinniformis, edwardsi, erubescens, golaia, labifera, modesta, mortenseni, muta, notha, opisthidia, pallida, pardalis, paroa, phoca, purcina, rubra, tristis, voniheringi, yaeyamensis, ylva, zibethina*) and 10 *Peltodoris* species (*aurea, crucis, hummelincki igla, nobilis, lancei, lentiginosa, lippa, punctifera, sauvagei, sordii*) which, under the *ICZN*, must all be re-allocated to a different genus. *Anisodoris* species binomials (*flindersi, sibogae, worki*) and *Diaulula* species binomials (*aurila, greeleyi, punctuolata, sandiegensis*) are no less problematic, because *Anisodoris* and *Diaulula* are not monophyletic (the type species of *Anisodoris* and *Diaulula* belong to the large, metaphyletic group at the base of *Discodorididae*).

Those problematic cases are handled in two ways:

(A) The first fully satisfies the *ICZN* rules, but is incompatible with phylogenetic principles. The genus name "*Montereina*" is used as the first part of the Linnaean binomial for all species that belong to the metaphyletic group at the base of *Discodorididae* and cannot be placed in any discodorid subclade of generic rank. "*Montereina*" is cited between quotation marks because it does *not* refer to a monophyletic taxon. This is compatible with the *ICZN* rules (the first part of the species combinations *must* be a name of genus rank), but is clearly not compatible with phylogenetic principles because it forces us to use a genus name that does not refer to a clade. The type species of the genus *Montereina* is *Montereina nobilis* (MacFarland, 1905). *Montereina* was selected among several generic names for several reasons: 1) *Diaulula*, of which the type species, *Diaulula sandiegensis*, is also part of the metaphyletic group of species at the base of *Discodorididae*, has been used exclusively for caryophyllidia-bearing species so far (Valdés and Gosliner 2001), and it might be disturbing to use it for all basal discodorids; 2) the type species of *Anisodoris*, *Anisodoris punctuolata*, also is a caryophyllidia-bearing dorid (Valdés and Gosliner 2001); 3) *Fracassa zibethina*, the type species of *Zibethina*, also belongs to this metaphyletic group at the base of discodorids, but it is a *nomen dubium*. Another option would be to create a new, monotypic genus name for each species in the metaphyletic group at the base of *Discodorididae*, i.e., 50 monotypic genera!

(B) The second is compatible with phylogenetic principles but does not satisfy the provisions of the *ICZN*. All species that belong to the metaphyletic group at the base of *Discodorididae* are referred to by using that clade name in front of the specific name: e.g., *Discodoris labifera* becomes *Discodorididae labifera*. The name *Discodorididae labifera* conflicts with *ICZN* rules, but is compatible with the approach proposed in the *ICPN* (Dayrat et al. 2008).

DISCUSSION

Infra-specific Character Variation

Most information on infra-specific variation described in this monograph is new, because it is the first time that so many specimens are dissected with the targeted goal of addressing infra-specific variation of all anatomical characters used for delineating discodorid species. Observations show that most characters traditionally used in the literature to distinguish species vary a great deal among individuals and should only be used if a significant number of specimens has been observed: color, number of rhinophoral lamellae, number of branchial plumes, radular formula, presence of denticles on radular teeth, relative size of the spermatic pouches, length and shape of the genital ducts, penial morphology, morphology of the spine of the accessory reproductive gland (if present), etc. It is difficult to evaluate how many specimens constitute a "significant" number of specimens to address infra-specific variation. However, based on the present work, it is estimated that five specimens would be a reasonable minimum.

However, the fact that characters vary infra-specifically does not mean that they cannot be used for distinguishing species. Rather, it means that, again, a sufficient number of specimens have been dissected in order to determine which features are really diagnostic, and their range of variation. The penial morphology is one of the best features one can find to distinguish species (when the penis is present, of course), but its variation in size and shape needs to be evaluated before it can be regarded as diagnostic.

Also, some characters that have been traditionally regarded as 'clear-cut' separation between species should be taken with much caution. For example, jaws are usually absent *or* present in a given species, but jaws are also exceptionally absent in species where they are normally present (see, e.g., *Sebadoris nubilosa*), and exceptionally present in species where they are normally absent (see, e.g., *Discodorididae aurila*). Again, this does not mean that the presence/absence cannot be used in delineating or distinguishing species: rather, it means that one should probably not use one (or just a few) specimen(s) to determine whether or not species is new based on this criterion.

Finally, it was frequently encountered that species descriptions published in the literature include many specimens listed as "examined," although only one or a few specimens were actually dissected (with no clear indication of this in the text). This is problematic and misleading. Indeed, if many specimens are listed as "examined," then the reader might think that the authors have actually dissected many specimens, when, in reality, authors have collected data from only one or a few specimens. For that reason, it is critical that authors actually specify clearly which specimens have been dissected, and which organs or structures have been mounted on SEM stubs. Without this information, it is difficult to evaluate the depth and rigor of any taxonomic work.

Estimation of Species Diversity

Prior to the present revision (Appendix 1), 85% of the names considered were regarded as valid (106 names out of 125 in total), 10% were regarded as synonyms (13 names), and 1.6% were regarded as *nomina dubia* (2 names). After the present revision, only 31% are valid (39 names), 30% are synonyms (37 names), 22% are *nomina dubia*, and 14% are names that refer to poorly-known species (18 names). These numbers confirm the critical need for taxonomic revisions in order to reach any good knowledge of the biodiversity of a given group. Without a revision, species names might be highly misleading, especially in taxa that have remained problematic for a long time such as discodorids. These data also suggest that names must not be taken for granted when estimating species diversity, especially if a group was not revised. The fact that the diversity in terms of valid species names has decreased a great deal through the present study is largely related to the specificities of *Discodoris*, which is a very large taxon that has remained a "garbage-can" for many years. However, there are quite a few new species of basal discodorids that have never been described; also, in dorids generally speaking, most studies tend to show that diversity is higher than what we currently know.

Before the present revision, most *Discodoris* species names were misleading, because their status was unknown. One of the goals of this revision was to determine the status of all available species names, and therefore sort the names that should be considered in biodiversity estimation (valid names), and names that should not be considered in biodiversity estimation (synonyms, *nomina dubia*). This revision does not help estimate the exact number of species in *Discodorididae* because many species have not been included in the revision (the present monograph focused on *Discodoris* and *Peltodoris*). However, estimates can be proposed for the taxa that have been studied in detail:

Discodoris includes three species, one of which remains unnamed (*boholiensis*, *cebuensis*, sp. A).

Peltodoris includes three species (*atromaculata*, *mullineri*, *murrea*)

Tayuva includes at present one species, *lilacina*. However, species delineation within *Tayuva* needs to be addressed with non-morphological data.

Sebadoris includes two species (*fragilis*, *nubilosa*). It cannot be excluded that *fragilis* and *nubilosa* could each refer to more than one species, but at this stage there is no positive evidence that there are more than two species.

Asteronotus currently includes four valid names: *cespitosus*; *raripilosa*, transferred here to *Asteronotus*; *mimeticus* Gosliner and Valdés, 2002; and *spongicolus* Gosliner and Valdés, 2002.

The new taxon *Hiatodoris* includes only two species (*fellowsi*, and the unnamed species sp. B).

At this stage, it is not possible to determine exactly how many species of *Paradoris* there are, but it should be at least eight or ten species (Dayrat 2006; Camacho-García and Gosliner, 2007).

The diversity of *Geitodoris* will be discussed in a separate revision (manuscript in preparation).

Rostanga clearly needs to be revised. It seems to be a large group. The taxonomy of *Rostanga* species is complicated because many species have the same dorsal color (homogeneously orange-red). Its delineation is also not obvious, because a few species have been placed in *Rostanga* although they do not have its characteristic, very elongate radular teeth (e.g., *aureamala*, *elandsia*, and *setidens*; see Garovoy et al. 2001). For sure, *Rostanga* is not an easy group.

Finally, there is a large group of 50 species names at the base of *Discodorididae*: among which 21 valid species, 17 *nomina dubia*, and 12 poorly known species (see above). Those 50 names do not constitute the totality of the species names that belong to the metaphyletic group at the base of *Discodorididae*. One should probably include a few additional *Diaulula* species names (e.g., *Diaulula cerebralis* Valdés, 2001; *Diaulula farmersi* Valdés, 2004). This metaphyletic group mainly includes species formerly classified in four genera: *Discodoris*, *Peltodoris*, *Anisodoris*, and *Diaulula*. If we do not count the *nomina dubia*, we obtain at present an estimation of at least 30 species in the metaphyletic group at the base of the *Discodorididae*.

Names of Doubtful Application

In this revision, many *nomina dubia* (27 names, i.e., 22%) were found. It is possible that future workers will think that some of those names are valid. However, it is unlikely because nothing is available for identification: the original descriptions are too incomplete, the types are either destroyed or lost. Many problematic (poorly-known species) names were also found (18 names, i.e., 14%): those names refer to species for which the original description provides some information that might help for re-identification, but for which, unfortunately, additional material was not available; in several cases, however, re-identification will be complicated, and many of those poorly-known species names will likely become *nomina dubia*.

In any case, as of today and based on the present monograph, 22% of the names considered here are *nomina dubia*. The main problem with the nomenclatural status of *nomen dubium* is that it can hardly be translated into any taxonomic reality and they can be potentially misleading. In that regard, *nomina dubia* are quite different from synonyms. Indeed, the taxonomic meaning of synonyms is known: synonyms are names that refer to the same entity (the important point being that we know which entity is actually referred to by synonyms). On the contrary, it is unknown what entity a *nomen dubium* refers to because, by definition, *nomina dubia* are "names of doubtful application." So, *nomina dubia* are still nomeclaturally available under the *ICZN*, but they do not have any taxonomic meaning. More importantly, if they are not recognized as *nomina dubia*, the latter can be quite problematic: indeed, names of doubtful application, often listed in checklists, are commonly used by ecologists and other people who have to deal with biodiversity estimates; however, *nomina dubia* introduce a bias in biodiversity estimations (they count as a "species"when they are just a name with no taxonomic meaning, although they are still available fron a nomenclatural standpoint). Only taxonomic revisions can clear this confusion.

The next question is what should we do with those names? Should we just forget about them? Indeed, one could argue that *nomina dubia* could just be dropped from any future work. However, because of the nature of any scientific endeavor, we cannot be certain that *nomina dubia* will ever become either valid names or synonyms, and so, unfortunately, those names should probably be kept available. This being said, it would be a good idea to exclude *nomina dubia* from biodiversity estimations and not confuse them with species names of which the application is not doubtful.

Lessons from history

Our current species descriptions will be regarded as incomplete a hundred years from now: whether or not we like it, our current standards for species description will look weak compared to future standards. Indeed, standards evolve: most of today's new species descriptions include SEM pictures of radular teeth, but Eveline and Ernst Marcus (in the 1960s) did not consider SEM to be indispensable, and Bergh (at the end of the 19th century) did not even have access to it. This justifies that we should think of guidelines for describing and naming new species (Dayrat 2005b).

In particular, it would probably be a good thing that new species names could be create based on several specimens to make sure that future workers have the possibility to dissect additional specimens. The example of *Discodorididae labifera* (Abraham, 1877) illustrates perfectly the situation: based on the original description, it is impossible to determine what the name refers to. However, one of the three syntypes was dissected and it was found that the penis was completely distinct from everything else that was known. Therefore, *labifera* is a valid name: if Abraham had described this species based on a single specimen and that the specimen had been destroyed or lost, then *labifera* would likely have become a *nomen dubium*. Other reasons why it seems appropriate to use multiple specimens to describe new species are: 1) we all commonly make mistakes in anatomical descriptions, and those mistakes can only be corrected if some original material (e.g., paratypes) is available for future workers; 2) it is the only way to address infra-specific variation. This being said, it is difficult to estimate how many specimens constitute a reasonable number: based on the present monograph, it is thought that five specimens should be a sufficient number, although a much larger sample would of course be ideal.

It seems also critical that we make available to future workers the type material (and original, not type, material) in its entirety, especially if it is all dissected so that future workers can look for novel characters. Several species have been described recently with just the body wall deposited in a museum (the SEM stubs with the radula was not deposited; the reproductive system was destroyed, the penis was lost, etc.). Such material becomes almost as uninformative as no type material deposited.

Therefore, we should think about species descriptions as if we were to be taxonomists in 150 years and ask ourselves: what is it that we do not describe or do today that people might be glad to find in museum collections 150 years from now? We would all be glad if Bergh had always described species based on 10 specimens all deposited in a museum collection. Today, we can reasonably predict (and hope) that sequencing a few markers is soon going to become part of standard taxonomic practices. So, it is going to become important to include a partial CO1 sequence of the type specimen in new species descriptions, so that future workers can include sequences of types in molecular analyses.

For all those reasons, several new species are described here but not named. Other workers would have probably named them (based on the argument that names help give existence to a species). However, those new species are currently insufficiently known. However, it is better to describe what is known about them without naming them than keeping those descriptions in a hard drive until new specimens become available. By starting to describe those new species, people know that they exist, but they also know that we need more information and specimens before we create actual new names, if needed.

Biogeography

Because the phylogenetic relationships among subclades of *Discodorididae* are still largely unknown, although some authors might disagree —Valdés and Gosliner (2001) proposed that the caryophyllidia-bearing dorids form a monophyletic taxon—, the possible biogeographical conclusions that can be drawn from the present results are limited. However, a few comments can be made. Three clades are purely tropical Indo-West Pacific clades, at least at this stage: *Discodoris* (*boholiensis*, *cebuensis*, and sp. A), *Sebadoris* (*fragilis* and *nubilosa*), and *Asteronotus* (*cespitosus* and *raripilosa* sampled here). *Peltodoris* is represented worldwide (except Arctic and Antarctic), which includes *atromaculata* (Mediterranean), *mullineri* (eastern Pacific), and *murrea* (tropical Indo-West Pacific). Several large clades (such as *Paradoris*, *Geitodoris*, *Platydoris*, *Rostanga*) have a worldwide distribution (except Arctic and Antarctic). Finally, an interesting distribution is that of *Hiatodoris*, with, so far, one species in Hawaii (*fellowsi*) and one species in the Galapagos (sp. B).

We cannot assert that Indo-West Pacific clades will remain exclusively restricted to that biogeographic region, but there seems to be a few clades (at least *Discodoris*, *Sebadoris*, *Asteronotus*, and *Halgerda*) that might have originated in the tropical Indo-West Pacific. Also, in absence of any fossil record, we cannot know whether or not those Indo-West Pacific clades have lived in any other regions. It is not possible to address the age of those clades at this stage.

Finally, it is difficult to give any general treatment about species distribution as our knowledge of the distribution of most species is biased because of unbalanced collecting efforts. Most well-known species, however, seem to have a broad distribution (e.g, *Sebadoris fragilis*), although endemic species definitely exist (e.g., *Discodorididae* sp. B).

Phylogenetic Relationships Within *Discodorididae*

Most discodorid clades (except for a few clades such as *Paradoris* and *Platydoris*) are currently delimited based on just one or few anatomical features. The fact that most authors agree on those delineations is a good sign. However, we must remain honest: most discodorid clades (*Discodoris*, *Peltodoris*, *Sebadoris*, etc.) are weakly supported (Dayrat and Gosliner 2005), which mainly is the result of the fact that good, discrete characters are difficult to find at this hierarchic level. Also, we still know little about a few potentially important features, such as the presence of hollow spine in the female accessory gland: such spines seem to be present in several groups, but we ignore the exact distribution of that character in discodorids. Finally, the 'value' of our anatomical features has never been tested through an *independent* test, i.e., with non-anatomical data. This is a big problem in groups like discodorids where the number of characters taxonomically useful is limited. Do we really test the phylogenetic value of characters when we use a cladistic method to reconstruct relationships but only use anatomical data, and that clades are supported by only one or two synapomorphies? The relationships among subclades of *Discodorididae* and within the metaphyletic group at the base of *Discodorididae* are still largely unknown, at least based on the present work.

Future Studies

Species delineation and discovery

In most cases, in the context of the present monograph, species could be delineated based on morphological features, and many more species of discodorids will be discovered in the future just by using morphology, especially criteria such as color and genital anatomy. However, it is always possible that morphospecies might contain cryptic species that we cannot distinguish with morphology. Indeed, several species (e.g., *Discodorididae coerulescens*) contain variants that diverge radically from the average morphology, suggesting possible cryptic species. More importantly, in some cases, morphology alone does not help draw limits between species, such as in *Tayuva*. There may be only one worldwide *Tayuva* species (*Tayuva lilacina*), or several species, e.g., one in the Mediterranean (*maculosa*), one in western Atlantic (*hummelincki*), one in tropical eastern Pacific (*ketos*), and one or more species in the tropical Indo-West Pacific (*lilacina*). In such cases, species limits will need to be addressed with phylogeography (e.g., by sequencing a few markers traditionally used at this level, such as CO1, 12S, 16S, and 28S).

Anatomical exploration

Although quite a few species are redescribed here, several species for which few specimens were available will still need to be anatomically redescribed, especially all the species regarded as poorly known, such as, *Discodorididae aurea* (Eliot, 1903), *Doridina edwardsi* (Vayssière, 1902), *Discodorididae flindersi* (Burn, 1962), *Discodorididae golaia* (Marcus and Marcus, 1966), *Doridina prea* (Marcus and Marcus, 1967), *Discodorididae sauvagei* (Rochebrune, 1881), and *Discodorididae ylva* (Marcus, 1965). Generally speaking, it is obvious that a vast anatomical diversity still remains to be described. This monograph includes comments on many unsuspected variations in key organs, such as the radula and the reproductive system, about which we still know very little. For instance, it seems that a much greater diversity of copulatory organs will likely be discovered in discodorids and dorids as a whole in the future, when more groups are revised and more species redescribed and discovered.

SPECIES DESCRIPTIONS

Discodoris Bergh, 1877

Under the *ICZN*, *Discodoris* is a taxon of genus-level. Type-species: *Discodoris boholiensis* Bergh, 1877, by subsequent designation by O'Donoghue (1926:207).

The phylogenetic diagnosis of *Discodoris* includes three classes of characters with different phylogenetic significance: 1) At present, one synapomorphy exclusively found in this taxon, i.e., the elongated shape of the tooth hooks (see character #17); only this synapomorphy of *Discodoris* can be regarded as diagnostic of this taxon (i.e., only the shape of the radular teeth can be used to identify a species that belongs to *Discodoris*); 2) Four synapomorphies of *Discodorididae*: a notched upper lip of the bilabiate anterior foot, digitiform or conical oral tentacles that are *not* expansions of the lateral mouth lips, a flattened prostate divided in two parts of distinct color, and two blood glands; and 3) Characters found in many other dorid nudibranchs, e.g., absence of rachidian teeth, hamate lateral teeth, etc. In addition, one character is found in some *Discodoris* species, but not all, i.e., a distinct, tridentate spur is present on the inner edge of the innermost tooth in *boholiensis* and *cebuensis*.

In the present contribution, *Discodoris* refers to a clade name, although it is not assigned to any particular rank. Under the *ICPN*, *Discodoris* is a converted clade name: it remains an informal clade name until it is phylogenetically defined *and* formally registered. *Discodoris* could be phylogenetically defined through an apomorphy-based definition as "the clade stemming from the first organism or species to possess an elongated, slightly curved tooth hook, as inherited by *Discodoris boholiensis* Bergh, 1877."

Discodoris boholiensis Bergh, 1877

Figures 3-11.

Discodoris boholiensis Bergh, 1877a:519-522, plate LX, fig. 23, plate LXI, figs 6-12.— Bergh, 1884a:92.— Bergh, 1890:897-900, plate LXXXVII, figs 28-31.— Bergh, 1905:99-100, plate I, fig. 9, plate XIII, figs 34-35, plate XIV, figs 1-2.— Eliot, 1903:364-365.— Rao, 1962:254-256, figs 2a-d.— Narayanan, 1968:199.— Lim and Chou, 1970:98, figs 1T, 7E.— Wells and Bryce, 1993:101, fig. 119.— Gosliner et al., 1996:159, fig. 557.— Debelius, 1996:247, unnumbered figure; Coleman, 2001:55, two unnumbered figures [the third picture of a specimen from PNG is probably a misidentification].— Valdés, 2002:565-566, figs 4D, 15-16.— Tonozuka, 2003:108, fig. 139.— Dominguez et al., 2004:104-105, fig. 3O.— Ono, 2004:133, fig. 271.— Berhens, 2005:25, 164, two unnumbered figures.

Discodorididae boholiensis.— Dayrat and Gosliner, 2005:205.

Asteronotus boholiensis (var.).— Risbec, 1928:107-109, fig. 23, plate IV, fig. 1.

Discodoris meta Bergh, 1877a:522-526, plate LX, figs 24-25, plate LXI, figs 25-26.— Bergh, 1884a:92.— Eliot, 1906a:554.

Type material (*boholiensis*).— Three syntypes (ZMUC GAS 2122): three specimens 70/40, 42/40, and 42/30 mm preserved, leg. Semper, 1861 [two specimens from Aibukit, Palau] and 1863 [one specimen from Bohol]. However, the two specimens from Palau cannot be distinguished from the specimen from Bohol.

Type material (*meta*).— Two syntypes (ZMUC GAS 2123): two specimens 55/41 and 39/31 mm preserved, leg. Semper, [no collecting date for the specimen from Cebu] and 1859 [specimen from Ubay].

Type material (*boholiensis* var.).— The eight syntypes could not be found.

Type locality (*boholiensis*).— The label currently indicates: Aibukit, Palau (?) (two syntypes), Bohol (one syntype). Authors have overlooked the fact that there are two type localities: Aibukit (07°38.4′N, 134°38.9′E) is in Palau; it also is called Ngebuked, Ngabuked or Gabbokkudo. Bohol is in the Philippines.

Type locality (*meta*).— Ubay [Bohol Island] (one syntype) and Cebu [Cebu Island] (one syntype), Philippines.

Type locality (*boholiensis* var.).— Port Despointes (one specimen) and Baie de Plum (seven specimens), New Caledonia.

Type material condition (*boholiensis*).— Bergh dissected the three syntypes. Pieces of dorsal mantle, digestive glands, one stomach (with a caecum), one intestine, one heart, six gills, and one uninformative reproductive system (only the female gland mass) remain in the jar.

Type material condition (*meta*).— Bergh dissected the two syntypes. The body walls, pieces of digestive glands, and six gills remain in the jar.

Additional material dissected.— **Madagascar**, Ile Sainte Marie, La Crique Hotel, 8 April 1990, one specimen 8/4 mm, leg. T. M. Gosliner, identified as *Discodoris boholiensis* by T. M. Gosliner (CASIZ 073543); **Australia**, Northern Territory, Darwin, Lee Point, 28 November 1976, one specimen 60/40 mm preserved length, leg. Richard Hamond (NMV F86409); Australia, Northern Territory, Gunn Point Beach, 12°11′N, 130°59′E, 13 November 1985, one specimen 16/14 mm preserved length, leg. C. Hood, identified *Discodoris boholiensis* by W. B. Rudman (AM C148492); **Coral Sea**, Osprey Reef, North Horn, 13°50′N, 146°33′E, 9 m depth, 15 December 1984, one specimen 20/8 mm preserved length, leg. Ian Loch, identified *Discodoris boholiensis* by W. B. Rudman (AM C144581); **Indonesia**, Sulawesi, Celebes Sea, Bunaken Island, off Manado, 9 m depth, 16 May 1990, one specimen 14/8 mm, leg. P. Fiene, identified as *Discodoris boholiensis* by P. Fiene (CASIZ 087129) [poorly preserved specimen]; **Papua New Guinea**, North coast, near Madang, Cement Mixer Reef, 24 October 1986, one specimen 20/15 mm preserved length, leg. M. Ghiselin, identified as *Discodoris boholiensis* by T. M. Gosliner (CASIZ 073520); Papua New Guinea, Milne Bay Province, Basilisk Point, northern coast of peninsula, 10°15.65′S, 150°42.75’, 6 to 10 feet depth, 28 May

1998, one specimen 35/20 mm preserved length, leg. T. M. Gosliner, identified as *Discodoris boholiensis* by T. M. Gosliner (CASIZ 113654); **Philippines**, Luzon, Batangas Province, Maricaban Island, Bethlehem, 8 May 2001, three specimens 45/25 (#1) mm, 40/20 (#2) mm, and 35/20 (#3) mm preserved length, leg. M. J. Adams, identified as *Discodoris boholiensis* by T. M. Gosliner (CASIZ 158768); Philippines, Palawan Island, North of Fondeado Island, 09°57′N, 118°55′E, 3-6 m depth, 6 May 1989, one specimen 20/12 mm preserved length, leg. A. G. Hinton & TAMS expedition, identified *Discodoris boholiensis* by W. B. Rudman (AM C158460); Philippines, Balabac Island, southwest end of Clarendon Bay, 07°48.5′ E 117°02′N, 30 feet depth, 16 June 1988, one specimen 18/15 mm preserved, leg. M. Campbell, identified as *Discodoris boholiensis* by T. M. Gosliner (CASIZ 071277); Philippines, NW Bohol Island, Danajon Bank, Banacon Island, 10°12′N, 124°10′E, February 1976, one specimen 70/50 mm preserved length, leg. C. Short & party, identified as *Discodoris* by W. B. Rudman (AM C104084); Philippines, Luzon, Batangas, Province, Maricaban Island, Devil's Point, 79 feet depth, 17 March 1994, one specimen 15/11 mm preserved length, leg. T. M. Gosliner, identified as *Discodoris boholiensis* by T. M. Gosliner (CASIZ 097404); Philippines, Luzon Island, Batangas, northern side of Sombrero Island, 19 February 1992, three specimens 55/45 (#1), 25/18 (#2), and 17/13 (#3) mm preserved length, leg. T. M. Gosliner, identified as *Discodoris boholiensis* by T. M. Gosliner (CASIZ 083654) [these specimens were dissected by Valdés (2002) prior to the present study; radulae and jaws are missing]; Philippines, Palawan Island, North of Hondo Baay, Tanabag Beach, 10°00′N, 119°01′E, 8 May 1989, one specimen 15/8 mm preserved length, leg. Ian Loch, identified *Discodoris boholiensis* by W. B. Rudman (AM C158450); **Japan**, Ryukyu Islands, Okinawa, 1.3 km ENE of Maeki-zaki, Seragaki Beach, 26°30.4′N, 127°52.6′E, 100 feet depth, 30 June 1989, one specimen 20/10, leg. Robert Bolland, identified as *Discodoris boholiensis* by T. M. Gosliner (CASIZ 070225).

DISTRIBUTION.— Indo-West-Pacific. Madagascar (Gosliner et al. 1996; present study), Zanzibar (Eliot 1903), Maldives (Eliot 1906a, as *meta*), Indian Ocean (Bergh 1890), Gulf of Kutch, western coast of India (Narayanan 1968), Andaman Islands (Rao 1962), Gulf of Mannar (Rao 1962), Singapore (Lim and Chou 1970), northern and northeastern Australia (Coleman 2001; present study), Indonesia (Bergh 1905; Debelius 1996; Coleman 2001; present study), Bali (Tonozuka 2003), Papua New Guinea (Gosliner et al. 1996; Dominguez et al. 2004; present study), Philippines (Bergh 1877a; Gosliner et al. 1996; Ono 2004; present study), Palau (Bergh 1877a), southern Japan (Gosliner et al. 1996; present study), New Caledonia (Risbec 1928), Vanuatu (Coleman 2001), Fiji (Gosliner et al. 1996). Note that Bergh (1877a:519) mentioned one specimen (the syntype collected in Bohol) collected from "deep water." This certainly means that the specimen simply was dredged or trawled, and probably not that it was found below 200 meters.

WWW.— The pictures posted on the *www* provide interesting information on the variation of the color of the dorsal notum. Most pictures were taken from the Philippines, Papua New Guinea and Indonesia. Other localities are worth noting: one specimen found crawling over sand, in Esperitu Santo, Vanuatu (Bill Rudman's *Sea Slug Forum* #1574, Vinka Stenhouse, December 19, 1999); one specimen collected on a coral platform in New Caledonia, in October 1993, during the field workshop organized by the Muséum national d'histoire naturelle in Koumac (Bill Rudman's *Sea Slug Forum* fact sheet *Discodoris boholiensis*, Bill Rudman, September 21, 1999); one specimen collected from Seragaki, Okinawa, on June 30, 1989, 30 meters depth (Robert Bolland's *Okinawa Slug Site*, December 22, 1997).

OCCURENCE.— It seems to be more common in the Philippines, Papua New Guinea and Indonesia, than in the rest of its distribution.

HABITAT.— Some specimens were found on coral rubble (CASIZ 070225, CASIZ 071852), on gray sponge (CASIZ 070225), on rock pools at low tide (NMV F86409), under rock on silty coastal reef (AM C158450), on slit and staghorn bottom in lagoon (AM C144581). According to Gosliner and co-authors (1996), *boholiensis* "feeds on sponges, but is also seen crawling about in the open or underneath rocks in relatively shallow water." Several authors mentioned *boholiensis* on reef (e.g., Bergh 1905; Coleman 2001).

Literature.— Most authors provided some information about the color and the morphology of the dorsal notum (e.g., Bergh 1877a, 1890, 1905; Eliot 1903, 1906a; Risbec 1928; Rao 1962; Wells and Bryce 1993; Gosliner et al. 1996; Debelius 1998; Coleman 2001; Tonozuka 2003; Ono 2004). In particular, the last four publications include color pictures. An uninformative drawing of the nervous system can be found in Risbec (1928) and some brief information about the radula can be found in Eliot (1903) and Risbec (1928). Other anatomical data can be found in Bergh (1877a, 1890, 1905) and Valdés (2002). However, character variation has never been addressed. Bergh (1884a) mentioned the names *boholiensis* and *meta* with no additional data.

Remarks on the original description (*boholiensis*).— Bergh simply mentioned that the notum is "broad … widely around the foot," (1877a:520) but did not point out that the mantle of *boholiensis* is distinctly more fragile, ample, and undulated than in other discodorid species. A piece of the dorsal notum of one syntype (70 mm long) was prepared for SEM; unfortunately, preservation had greatly damaged the notum and the tubercles are shapeless (Fig. 4A). Bergh (1877a:519-520) described the color thoroughly: "whitish or dirty yellowish-whitish or more dirty yellowish; the back was covered everywhere with tightly, compact round brown-black points (up to 0.25 mm); the median crest blackly speckled or covered with black spots; the back as well as the rim of the foot black, the first on top with short, and often wide inward-turned branches of this color, which speckle the outer portion of the mantle; the margin of the rhinophoral and gill sheaths black or blackly speckled; the club of the rhinophores brownish or blackish; the gills with blackish leaves, with whitish rachis; the tentacles black." Bergh mentioned several general features, such as six gills (two left and right halves of three) in one syntype and eight (two halves of four) in the two other syntypes, 80 rhinophoral lamellae (there are fewer lamellae), a bilabiate anterior foot with a grooved upper lip, a nervous system "somewhat as usual," a labial cuticle armed with jaw plates, and a radular formula (Fig. 5C) of 39/42 × (60/66-0-60/66). Bergh did not describe the position of the stomach: the type material has a median, narrow stomach, with a small caecum on its left, posterior side. Finally, Bergh (1877a:522) described the very long and highly convoluted deferent duct as a "thick, flattened, longish ball," and "no strong penis."

Remarks on the original description (*meta*).— The original description of *meta* is similar to the description of *boholiensis*, which makes sense given that Bergh thought that *meta* probably was just a variety of *boholiensis*. A few features are emphasized: 40 to 50 rhinophoral lamellae, six (or eight) branchial plumes, a radular formula of 41/42 × (56/60-0-56/60). Also, the radular teeth illustrated by Bergh for *meta* cannot be distinguished from the teeth of *boholiensis* (Figs. 5A-C).

Description of new specimens (Figs. 3-11).— *Color*: The ground color of the dorsal notum is whitish-yellowish but is abundantly covered with opaque white, dark red, brown, and black spots. The latter correspond to the apical parts of the tubercles. The margins of the notum are dark red, often interrupted by black and white areas (more or less linear) oriented towards the median line. The median keel, or crest, from the branchial opening up to the rhinophores, is blotched with brown, black and white; a white, irregular line often marks the top of the keel. The dark brown gills and rhinophores also bear white pigments. The dorsal color varies from light cream (e.g., CASIZ 071277) to very dark (e.g., CASIZ 070225). The hyponotum and the foot are creamish. The edge of the foot is dark red. The ground color of preserved specimens is usually creamish. However, the keel, the foot and notum edges, the rhinophores and the gills are still dark red. Also, the apex of some tubercles is still white or brown after preservation.

External morphology. The body is oval. Its length equals less than twice its width. The notum of *boholiensis* is thin and fragile. The dorsal notum bears tubercles that are not caryophyllidia. Many small holes (diameter < 10 μm) and many small tufts of cilia were found on the mantle,

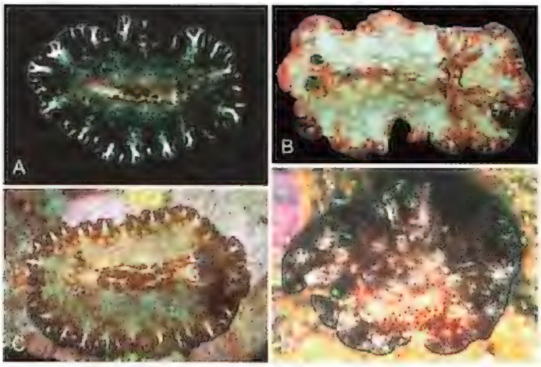

FIGURE 3 *Discodoris boholiensis*, dorsal color. A. CASIZ 070225 (R. Bolland).— B. CASIZ 071277 (M. Campbell).– C. CASIZ 083654 (T. M. Gosliner).— D. CASIZ 073543 (T. M. Gosliner).

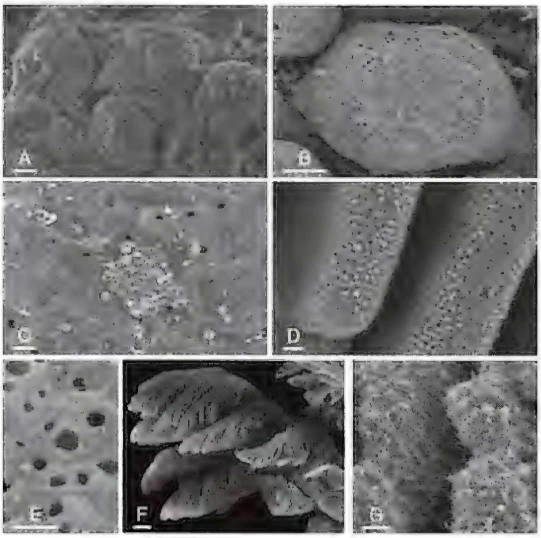

FIGURE 4. *Discodoris boholiensis*. A. Dorsal notum, tubercles, syntype, ZMUC 2122, scale = 100 µm.— B. Dorsal notum, tubercle, CASIZ 158768 (#1), scale = 100 µm.— C. Dorsal notum, tubercle (apex), CASIZ 158768 (#1), scale = 10 µm.— D. Rhinophoral lamellae, CASIZ 158768 (#1), scale = 20µm.— E. Dorsal notum, tubercle, detail, CASIZ 158768 (#1), scale = 10 µm.— F. Branchial plume, CASIZ 073520, scale = 200 µm.— G. Rhinophoral lamellae, CASIZ 070225, scale = 20 µm.

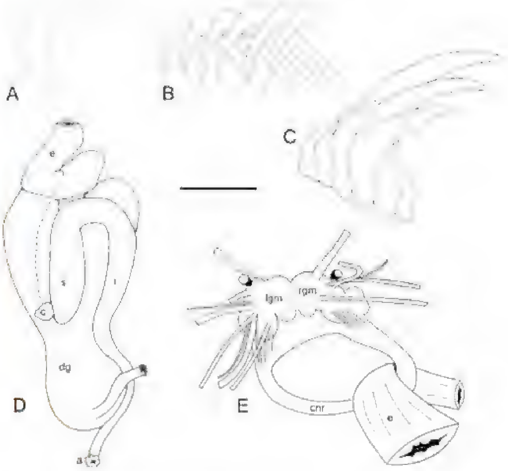

FIGURE 5. *Discodoris boholiensis*. A. Radular tooth of Discodoris meta, after Bergh (1877a: plate LXI, fig. 27).— B. Radular teeth of *Discodoris meta*, after Bergh (1877a: plate LXI, fig. 25).— C. Outermost teeth of *Discodoris boholiensis*, after Bergh (1877a: plate LXI, fig. 12).— D. Digestive system (without buccal mass), dorsal view, CASIZ 158768, scale = 5 mm.— E. Nervous system, dorsal view, CASIZ 158768, scale = 1.5 mm.

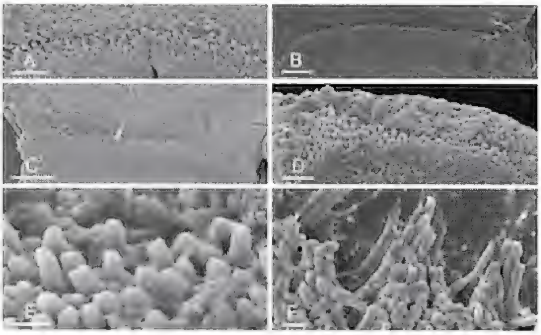

FIGURE 6. *Discodoris boholiensis*, labial cuticle with jaws. A. One lateral jaw plate, MV F86409, scale = 40 µm.— B. One lateral jaw plate, CASIZ 070225, scale = 60 µm.— C. One lateral jaw plate, AM C148492 scale = 100 µm.— D. One lateral jaw plate, AM C145581, scale = 40 µm.— E. Rodlets, AM C145581, scale = 10 µm.— F. Rodlets, CASIZ 158768 (#1), scale = 10 µm.

including the dorsal tubercles, the oral tentacles, the rhinophores and the gills. The foot is rounded posteriorly and anteriorly. The anterior foot is bilabiate and the upper lip is notched. The oral tentacles are digitiform, not grooved. In preserved specimens, the margins of the rhinophoral and branchial sheaths can be smooth or lightly crenulate. There are six tripinnate branchial plumes. The rhinophores have from 15 to 45 lamellae, depending on the size of the animal.

Digestive system. The stomach is free, median: it does not cover the left anterior part of the digestive gland; it is surrounded on both sides by the digestive gland. A caecum is present. The

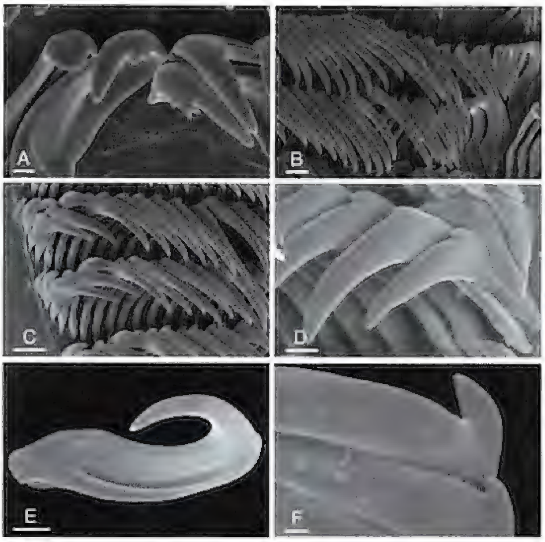

FIGURE 7. *Discodoris boholiensis*, radula. A. Innermost teeth, CASIZ 158768 (#1), scale = 10 µm.— B. Median teeth, CASIZ 158768 (#1), scale = 40 µm.— C. Outermost teeth, CASIZ 158768 (#1), scale = 60 µm.— D. Outermost teeth, CASIZ 158768 (#2), scale = 20 µm.— E. Median tooth, internal view, CASIZ 158768 (#2), scale = 20 µm.— F. Median teeth, detail, CASIZ 158768 (#2), scale = 5 µm.

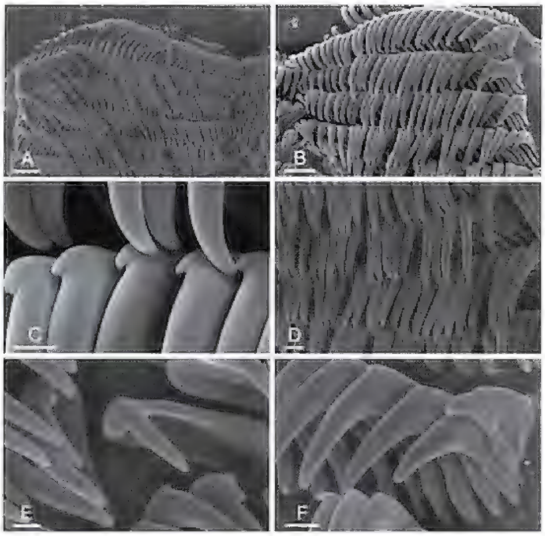

FIGURE 9. *Discodoris boholiensis*, radula. A. Left rows, CASIZ 073520, scale = 100 µm.— B. Right rows, CASIZ 097404, scale = 60 µm.— C. Median teeth, detail, CASIZ 097404, scale = 10 µm.— D. Median teeth, CASIZ 071277, scale = 100 µm.— E. Innermost teeth, CASIZ 071277, scale = 10 µm.— F. Outermost teeth, CASIZ 071277, scale = 20 µm.

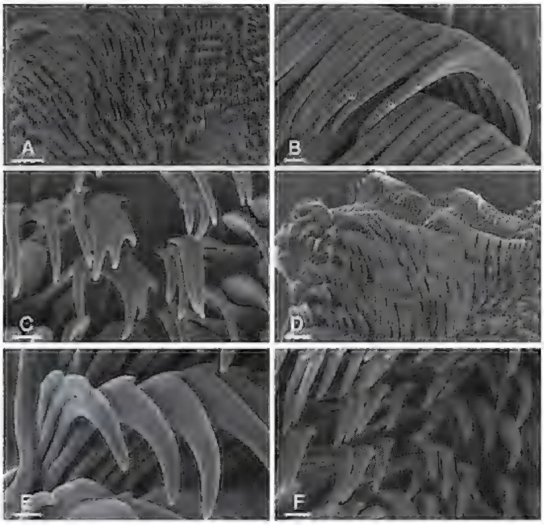

FIGURE 8. *Discodoris boholiensis*, radula. A. Left rows, AM C104084, scale = 200 µm.— B. Median teeth, AM C104084, scale = 30 µm.— C. Innermost teeth, AM C104084, scale = 40 µm.— D. Left rows, CASIZ 113654, scale = 100 µm.— E. Outermost teeth, CASIZ 113654, scale = 20 µm.— F. Innermost teeth, CASIZ 113654, scale = 20 µm.

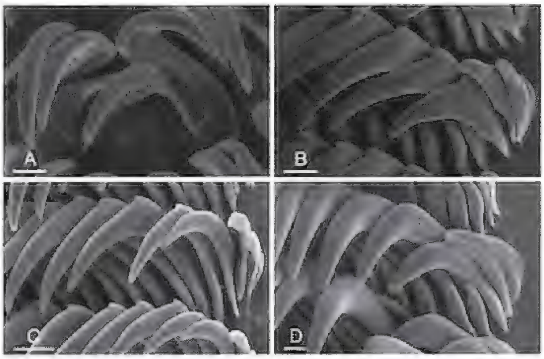

FIGURE 10. *Discodoris boholiensis*, radula. A. Innermost teeth, MV F86409, scale = 20 µm.— B. Outermost teeth, MV F86409, scale = 30 µm.— C. Outermost teeth, detail, CASIZ 070225, scale = 30 µm.— D. Outermost teeth, CASIZ 073543, scale = 10 µm.

intestine is straight and dorsal. The digestive gland is brightly pink in two specimens. The labial cuticle is armed with a pair of jaw plates. However, the jaws are difficult to see, especially under the dissecting microscope because of the red-brown color of the labial cuticle. SEM pictures show that the jaws are two narrow bands of a few rows of rodlets (maximum five rows, usually three). No strong, sickle-shaped jaw plate was found. The presence of rodlets is uncertain in one specimen (CASIZ 113654). The rodlet tips are irregular. The length of the radula equals less

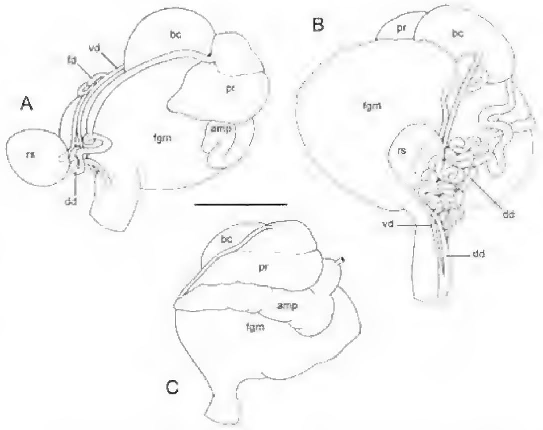

FIGURE 11. *Discodoris boholiensis*, reproductive system. A. CASIZ 073543, scale = 2 mm.— B. CASIZ 158768, scale = 5 mm.— C. CASIZ 158768, scale = 5 mm.

than twice its width. The radular sac cannot be seen by dorsal dissection. The radular formulae are: 10 × (17-0-17) in an 8 mm long specimen (CASIZ 073543), 12 × (28-0-28) in a 15 mm long specimen (CASIZ 097404), 16 × (27-0-27) in a 20 mm long specimen (CASIZ 070225), 17 (34-0-34) in a 20 mm long specimen (AM C144581), 20 (42-0-42) in a 17 mm long specimen (CASIZ 071277), 20 × (46-0-46) in a 35 mm long specimen (CASIZ 113654), 23 × (42-0-42) in a 20 mm long specimen (CASIZ 073520), 22 × (34-0-34) in a 16 mm long specimen (AM C148492), 24 × (43-0-43) in a 40 mm long specimen (CASIZ 158768 #2), 27 × (50-0-50) in a 60 mm long specimen (NMV F86409), 30 × (65-0-65) in a 70 mm long specimen (AM C104084), 35 × (46-0-46) in a 45 mm long specimen (CASIZ 158768 #1). The rachidian teeth are absent and the rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis. In the fully developed radulae, the size of the teeth gradually increases from the first innermost tooth up to the seventh or tenth lateral tooth, then stays approximately constant, and finally decreases for the last three or four outermost teeth. The last two outermost teeth are reduced, and often just triangular instead of hamate. In a young specimen (CASIZ 073543), the size of the teeth gradually increases up to the middle of the row, and then gradually decreases up to the two outermost teeth. The tooth hooks are significantly more elongated and thinner than in other species studied here. The teeth bear no outer denticles, but the first innermost tooth bears a strong, inner denticle with three tips. The foot of all lateral teeth has a wing on its inner, anterior edge. This wing can only be seen if a tooth is observed on its inner lateral view. In dorsal view, it appears as a strong spur on the inner edge of the tooth hooks. This spur is always present, although it is weak in the 8 mm long specimen (CASIZ 073543).

Nervous system. The circum-esophageal nerve ring is short; its length equals approximately twice the width of the two ganglia. The cerebral and pleural ganglia are fused.

Reproductive system. The ampulla is loosely straight, although it forms two loops before reaching the female gland mass in a small specimen (CASIZ 073542). The division between male and female ducts could not be seen by dissection. The prostate is divided in a proximal, whitish part and a distal yellowish part. The deferent duct is very long and highly convoluted. It has so many tight loops that it actually is difficult to follow the duct for its entire length. Two small specimens (not fully mature) had a much shorter deferent duct with a few loops easily distinguishable (CASIZ 071277, CASIZ 073542). However, a highly convoluted deferent duct was found in small individuals with a small, mature, reproductive system (e.g., AM C158460, AM C148492). The deferent duct and the vaginal duct join and share a common opening, but the latter is separate from the female opening. If there is a common general atrium, it is very short. No distal accessory gland and no distinct penial papilla were found. The vaginal duct is straight; one third of its length is hidden behind the deferent duct. The fertilization duct is loosely convoluted (it is S-shaped near the bursa copulatrix). The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is marked by a very short duct. The bursa copulatrix is about twice as large as the receptaculum seminis. The two spermatic pouches are ovate, and not attached.

Diagnostic features.— The color of the dorsal notum of *boholiensis* is diagnostic and can hardly be mistaken, although it varies among individuals (Wells and Bryce 1993; Gosliner et al. 1996; Debelius 1996; Coleman 2001; Tonozuka 2003). Potentially helpful internal characters are: 1) the general organization of the reproductive system with a highly convoluted deferent duct (acknowledging some variation in young individuals); 2) the denticle on the inner side of the innermost lateral tooth; 3) the tooth hooks significantly narrower and more elongated than usual; 4) the wing on the inner edge of the tooth feet (with the spur in dorsal view). Note, however, that these four features are also found in *cebuensis*, and thus not diagnostic of *boholiensis*.

Infra-specific character variation.— Anatomical and morphological data available in the literature are compatible with the range of variation observed here. The largest living animals known are 80 mm long (Risbec 1928) and 75 mm long (Rao 1962). The largest preserved animals known are 75 mm long (Bergh 1877a) and 70 mm long (AM C104084). The radular formulae found in the literature are: 22 × (40-0-40) in a 30 mm long specimen, alive (Narayanan 1968), 27 × (30-0-30) in a 40 mm long specimen (Bergh 1905), 29 × (35-0-35) in a 49 mm long specimen (Valdés 2002), 23 × (40-0-40) in a 62 mm long live animal (Eliot 1903), 27 × (46-0-46) in a 23 mm long specimen (Bergh 1890), 39/42 × (53/66-0-53/66) in specimens from 52 to 75 mm long (Bergh 1877a), 41/42 × (56/60-0-56/60) in a maximum 60 mm long specimen (Bergh 1877a, as *meta*), 25 × (60-0-60) in specimens up to 80 mm long, alive (Risbec 1928). In summary, the number of rows and number of teeth per half row vary from 10 (for 17 teeth per half row) in an 8 mm long specimen (CASIZ 073543) to 42 (for 66 teeth per half row) in a 75 mm long specimen (Bergh 1877a).

Discussion.— Risbec (1928) described a variety of *boholiensis* and re-allocated it from *Discodoris* to *Asteronotus*. He did not give a clear explanation, but it seems that the presence of a median crest on the dorsal notum of *boholiensis* motivated his decision. Several features indicate that Risbec was looking at real *boholiensis* specimens, not at *Asteronotus*: a very long and convoluted deferent duct, median crest bearing a z-shaped white line, important autotomy of the mantle, etc. Risbec thought that his eight Caledonian specimens were part of a variety distinct from Bergh's specimens because of three features: white lines on the rhinophores, a median crest with a well-marked z-shaped line, and a number of teeth reaching 120 per row instead of a maximum of 66 in Bergh's description. However, Bergh mentioned a maximum number of teeth of 66 per half row, not per row. Also, given the variation of the color of the dorsal notum of *boholiensis*, no new variety was needed. Note that Ros (1976a:46) cited Risbec's (1928) contribution for the autotomy of the mantle of *Discodoris boholiensis*, assuming that Risbec's generic classification was erroneous. Finally, Risbec (1928) proposed (though with a question mark) that *boholiensis* could be a synonym of *Doris intecta* Kelaart, 1859, but the latter is a distinct species, originally described within *Doris* and currently classified in *Atagema* (see Valdés and Gosliner 2001).

Eliot (1906a) mentioned a single specimen (23/17 mm preserved) that he identified as *meta* from the Maldives Archipelago. In the brief description of this specimen, Eliot mentioned a ground color "yellowish with remains of brown and purple blotches in the middle" as well as an "ample and undulated" (1906a:554) mantle. This description could match both *meta* and *boholiensis*, but one may argue that it still is a vague description. Regardless of whether or not Eliot's identification is a valid record, *boholiensis* is expected to be present in the Maldives.

The synonymy between *meta* and *boholiensis* seems to have been first formally proposed by Valdés (2002), based on notes taken by T. M. Gosliner at the Zoological Museum, University of Copenhagen.

Supra-specific relationships.— A phylogenetic test of the relationships of *boholiensis* shows that it is nested with two other species (*cebuensis* and an unnamed species described here, sp. A) within a clade. Because *boholiensis* is the type species of *Discodoris*, this clade can reasonably be called *Discodoris*, which implies that *Discodoris* cannot be used as a generic name for all the '*Discodoris*' species that are part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial for *boholiensis* should be *Discodoris boholiensis*, which is also a possible name under the *ICPN*.

Discodoris cebuensis Bergh, 1877

Figures 12-22.

Discodoris cebuensis Bergh, 1877a:526-528, plate LXI, fig. 13, plate LXII, figs 21-24.— Bergh, 1884a:92.— Eliot, 1910a:411, 422, 424.

Discodoris schmeltziana.— Bergh, 1880a:47-48, plate A, figs 15-19.— Bergh, 1884a:93.— Eliot, 1910a:422.— Dayrat and Gosliner, 2005:202, 204, 218, 224 [not *Doris schmeltziana* Garrett in Bergh, 1875].— Yonow, 2008:152, four unnumbered figures.

Discodorididae schmeltziana.— Dayrat and Gosliner, 2005:205 [not *Doris schmeltziana* Garrett in Bergh, 1875].

Discodoris sp. 2 Gosliner, 1987:64, fig. 76.

Discodoris sp. 3 Ono, 1999:106, fig. 170.

Discodoris sp. 2 Ono, 2004:136, fig. 275.

Type material (*cebuensis*).— Holotype (ZMUC GAS-2124), by monotypy: one specimen 26/17 mm preserved, leg. Semper, 1864.

Type material condition (*cebuensis*).— The holotype was dissected by Bergh. Few organs are left: digestive gland, six gills, flattened prostate and female gland mass. No slides could be found. The oral area is destroyed but one digitiform oral tentacle is still present.

Type locality (*cebuensis*).— Cebu, Philippines.

Additional material dissected.— **Tanzania**, Zanzibar, Ras Nungwi, 6 November 1994, one specimen 58/36 mm preserved, leg. Connie Boone, identified as *Discodoris* by T. M. Gosliner (CASIZ 099355) [this specimen was dissected prior to the present study, and the buccal mass was missing]; **Indonesia**, Moluccas, Banda Islands, Karang Hatta, 7 meters depth, 15 November 1993, one specimen 27/24 mm preserved, leg. Pauline Fiene, identified as Discodoris by T. M. Gosliner (CASIZ 093937) [this specimen is poorly preserved, and the reproductive system was destroyed prior to the present study]; Indonesia, Sulawesi, Lembeh Strait, Pulau Kecil, 6 m depth, 6 November 1993, one specimen 25/17 mm preserved, leg. Pauline Fiene, identified as *Discodoris* by T. M. Gosliner (CASIZ 097591) [this specimen was dissected prior to the present study; the buccal mass and the reproductive system were missing]; **Philippines**, Luzon, Batangas Province, Maricaban Island, Devil's Point, 20 meters maximum depth, 15 April 1996, one specimen 20/8 mm, leg. T.M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 106482); Philippines, Luzon Island, Batangas Province, Balayan Bay, Seafari Beach, 23 April 1997, one specimen 57/38 mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 110381); Philippines, Luzon Island: Batangas Province: Balayan Bay, Seafari Beach, 19 April 1997, one specimen 37/25 mm preserved, leg. Jeff Holmes, identified as *Discodoris* by T. M. Gosliner (CASIZ 110447); Philippines, Luzon Island, Batangas Province, Balayan Bay, Seafari Beach, night dive, 15 meters depth, 6 May 2001, one specimen 27/18 mm preserved, leg. A. Valdés, identified as *Discodoris* by T. M. Gosliner (CASIZ 156672); **Japan**, Ryukyu Islands, Okinawa, 1.3 km ENE of Maeki-zaki, Seragaki Beach, 26°30.4'N, 127°52.6'E, 5 feet depth, 12 May 1989, one specimen 55/35 mm preserved, leg. R. F. Bolland, identified a s *Discodoris* by T. M. Gosliner (CASIZ 070018); Japan, Ryuku Islands, Okinawa, 26°17.8'N, 127°54.3'W, 18 May 1989, one specimen 85/55 mm preserved, leg. Robert F. Bolland, identified as *Discodoris* by T. M. Gosliner (CASIZ 070019); **Hawaii**, Maui, about 2 km west of Maalaea marina, 4 October 2003, one specimen 25/15 mm preserved (in ethanol 95%), leg. Cory Pittman, identified as *Discodoris* by T. M. Gosliner (CASIZ 168013).

Distribution.— Indo-West Pacific: Red Sea (Yonow 2008), South Africa (Gosliner 1987, as *Discodoris* sp. 2), Tanzania (present study), Seychelles (Eliot 1910a, as *cebuensis*), Indonesia (present study), Papua New Guinea (see below, *www*), Philippines (Bergh 1877a, as *cebuensis*; present study), Japan (Ono 1999, as *Discodoris* sp. 3; Ono 2004, as *Discodoris* sp. 2; present study), Society Islands (Bergh 1880a, as *schmeltziana*), Hawaii (present study).

OCCURRENCE.— Ten specimens are mentioned in the present study, which means that, so far, a total of fourteen specimens were recorded in the literature (Bergh 1877a; Bergh 1880a; Gosliner 1987; Ono 1999; present study). Some additional pictures of *cebuensis* (as *schmeltziana*) have recently been posted on the *www*.

HABITAT.— Under rocks (CASIZ 097591, CASIZ 168013), on coral rubble (CASIZ 070018), on mixed silty sand, rocks and coral rubble (CASIZ 070019).

WWW.— A few pictures of *cebuensis* (as *schmeltziana*) have recently been posted on Bill Rudman's *Sea Slug Forum*. Those specimens were collected from Hawaii (Maui and Oahu), and Papua New Guinea (Gonubalabala Island).

LITERATURE.— Bergh's original description of *cebuensis* is the only anatomical description available, although Eliot (1910a) briefly described the external morphology and the radular formulae of two specimens that he identified as *cebuensis*. Eliot (1910a:422) mentioned the existence of *schmeltziana* without adding new data. A few color pictures can be found in the literature (Gosliner 1987; Ono 1999, 2004).

REMARKS ON THE ORIGINAL DESCRIPTION (*cebuensis*).— Bergh mentioned several general features, such as a bilabiate anterior foot with a notched superior lip, 30 rhinophoral lamellae, two jaw plates, hamate lateral teeth, and a radular formula of 30 × (36-0-36). Bergh's description of the shape of the teeth is detailed and important: the inner edge of the innermost tooth bears a denticle; the inner edge of the lateral teeth bears a pointed spur that actually corresponds to a wing that runs along the dorsal, inner edge of the tooth foot; finally, the two outermost teeth have a wide base, and are almost triangular, not elongated and thin (Figs. 15D-E). Bergh's description of the color is problematic because he did not know the color of the live animal: a dorsal notum with a yellowish-white ground color, brownish-grey spotted; hyponotum and foot sole with dots too; brownish-grey rhinophores with yellowish tips; yellowish gills. The current color of the holotype is yellowish-pinkish. SEM pictures confirm that the dorsal tubercles are not caryophyllidia (Fig. 13A). The dorsal tubercles are tightly close to each other and several of them are significantly larger than the others (this feature was not mentioned by Bergh); six of those larger tubercles are arranged in two rows of three tubercles between the rhinophores and the gills.

MORPHOLOGICAL DESCRIPTION OF NEW SPECIMENS (Figs. 12-22).— *Color*. The dorsal notum of living animals bears white and red-brown indefinite blotches and a few blue larger tubercles (CASIZ 110381, CASIZ 099355, CASIZ 070018, CASIZ 070019, CASIZ 097591, CASIZ 106482, CASIZ 156672). Typically, there is a dark red margin around the notum interrupted by patches of several white tubercles and a larger blue tubercle. Also, three to five larger blue tubercles are arranged in the median part of the notum. The number and the arrangement of the large, blue tubercles vary among individuals. The pattern of whitish and red-brown areas varies among individuals as well. The Preservation greatly modifies the color. In particular, the large, blue tubercles remain larger than the other regular tubercles after preservation, but most often are colorless (except for recently collected specimens). The different whitish and red-brown areas are still distinct. The ventral surface, whose ground color is creamish-yellowish, bears some dark brown dots that can still be observed after preservation.

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform and not grooved. The dorsal notum bears tubercles that are not caryophyllidia. Many small holes (diameter < 10 μm) and many tufts of cilia are present on the dorsal surface, including the rhinophores and the gills. In preserved specimens, the

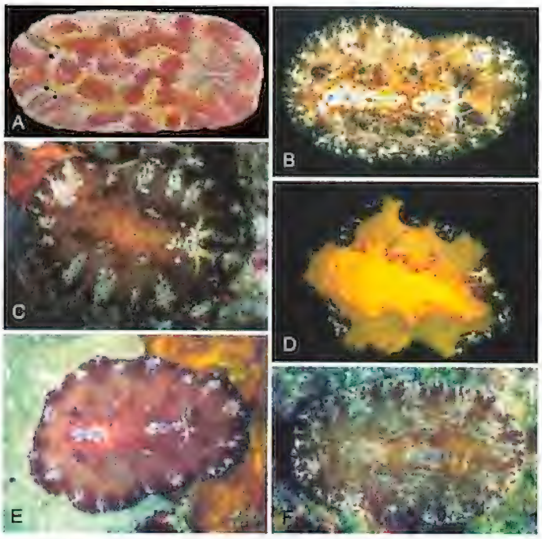

FIGURE 12. *Discodoris cebuensis*. A. Dorsal color, *Discodoris schmeltziana* (Bergh, 1880a: plate A, figs 15), not *Doris schmeltziana* Garrett in Bergh, 1875.— B. Dorsal color, CASIZ 070018 (R.F. Bolland).— C. Dorsal color, CASIZ 110381 (T.M. Gosliner).— D. Ventral color, CASIZ 070018 (R.F. Bolland).— E. Dorsal color, CASIZ 106482 (T.M. Gosliner).— F. Dorsal color, CASIZ 156672 (A. Valdés).

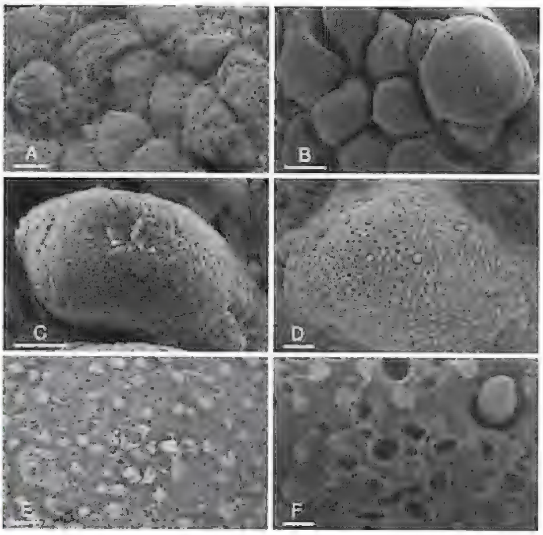

FIGURE 13. *Discodoris cebuensis*, dorsal notum, tubercles. A. Holotype of *cebuensis*, ZMUC 2124, scale = 100 µm.— B. CASIZ 110447, scale = 400 µm.— C. CASIZ 110447, scale = 200 µm.— D. CASIZ 110381, scale = 50 µm.— E. CASIZ 110381, scale = 20 µm.— F. CASIZ 110381, scale = 10 µm.

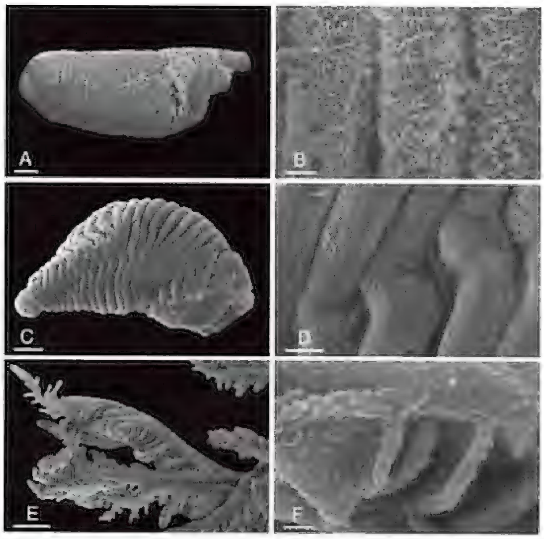

FIGURE 14. *Discodoris cebuensis*. A. Rhinophore, CASIZ 070019, scale = 400 µm.— B. Rhinophoral lamellae, CASIZ 070019, scale = 30 µm.— C. Rhinophore, CASIZ 156672, scale = 200 µm.— D. Rhinophoral lamellae, CASIZ 156672, scale = 40 µm.— E. Branchial plumes, CASIZ 156672, scale = 300 µm.— F. Branchial plume, detail, CASIZ 156672, scale = 40 µm.

margins of the rhinophoral and branchial sheaths are smooth or lightly crenulate. There are six tripinnate branchial plumes. The rhinophores have from 22 to 40 lamellae, depending on the size of the animal.

Digestive system. The stomach is free, large, on top of the left, anterior side of the digestive gland. A caecum is present. The intestine is straight and dorsal. The labial cuticle is armed with a pair of lateral jaw plates. Rodlet tips are irregular. The radula is from one and a half to two times longer than wide. The radular sac cannot be seen by dorsal dissection. The radular formulae are: 18 × (22-0-22) in a 20 mm long specimen (CASIZ 106482), 21 × (32-0-32) in a 37 mm long specimen (CASIZ 110447), 22 × (40-0-40) in a 27 mm long specimen (CASIZ 093937), 25 × (30-0-30) in a 57 mm long specimen (CASIZ 110381), 25 × (35-0-35) in a 25 mm long specimen (CASIZ 168013), 25 × (28-0-28) in a 27 mm long specimen (CASIZ 156672), 35 × (50-0-50) in a 85 mm long specimen (CASIZ 070019). The radular formula of a 55 mm long specimen (CASIZ 070018) was 15 × (33.0.33), but the radula was not complete because several rows were lost during the preparation. The rachidian teeth are absent and the rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the teeth gradually increases from the rachis to the edges, except for the three or five outermost teeth, which are much smaller than the rest of the lateral teeth. The last outermost teeth are triangular, with a wide base. The tooth hooks are significantly thinner than in other species dissected here (except for *boholiensis*, which has a similar radula). The teeth bear no denticles, except for the first innermost tooth that has a strong denticle on its inner edge. This denticle, which can have several tips, is always present. The foot of all lateral teeth has a wing on its inner, dorsal edge, from the radular membrane to the hook. This wing can only be seen if a tooth is observed on its inner lateral view. In dorsal view, it appears as a strong spur on the inner edge of the teeth. This spur is always present.

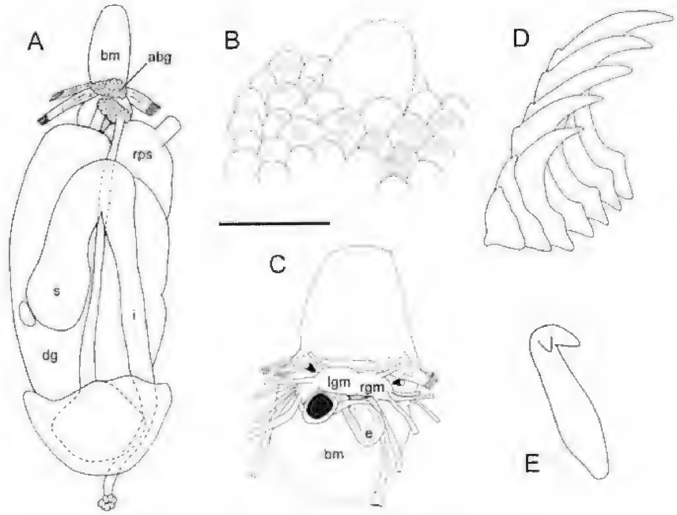

FIGURE 15. *Discodoris cebuensis*. A. General anatomy, CASIZ 110381, scale = 6.5 mm.— B. Dorsal notum, tubercles, CASIZ 110381, scale = 2.5 mm.— C. Central nervous system and buccal mass, CASIZ 110381, scale = 2.5 mm.— D. Outermost teeth, after Bergh (1877a, plate LXII, fig. 23).— E. Innermost tooth, after Bergh (1877a, plate LXII, fig. 21).

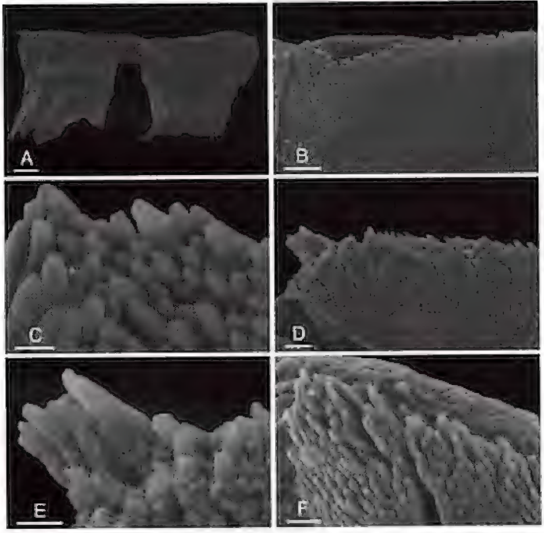

FIGURE 16. *Discodoris cebuensis*, jaws. A. Pair of lateral jaw plates, CASIZ 070018, scale = 200 µm.— B. Right, lateral jaw plate, CASIZ 070018, scale = 30 µm.— C. Jaw rodlets, CASIZ 070018, scale = 10 µm.— D. Jaw rodlets, CASIZ 070019, scale = 20 µm.— E. Jaw rodlets, CASIZ 070019, scale = 10 µm.; F. Jaw rodlets, CASIZ 156672, scale = 20 µm.

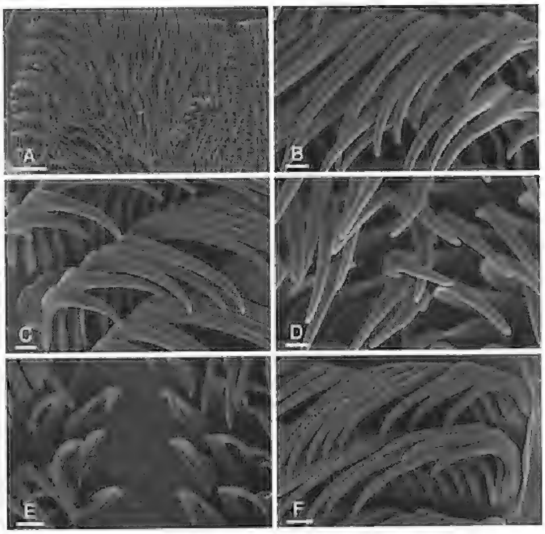

FIGURE 17. *Discodoris cebuensis*, radula. A. Left rows, CASIZ 070019, scale = 200 µm.— B. Median teeth, CASIZ 070019, scale = 30 µm.— C. Outermost teeth, CASIZ 070019, scale = 30 µm.— D. Innermost teeth, CASIZ 070019, scale = 20 µm.— E. Innermost teeth, CASIZ 070018, scale = 40 µm.— F. Outermost teeth, CASIZ 070018, scale = 40 µm.

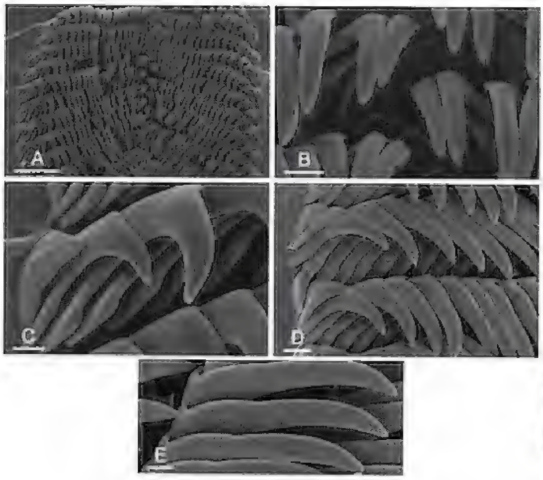

FIGURE 18. *Discodoris cebuensis*, radula. A. Anterior half, CASIZ 106482, scale = 200 µm.— B. Innermost teeth, CASIZ 106482, scale = 20 µm.— C. Outermost teeth, CASIZ 106482, scale = 20 µm.— D. Outermost teeth, CASIZ 110381, scale = 40 µm.— E. Median teeth, detail, CASIZ 110381, scale = 20 µm.

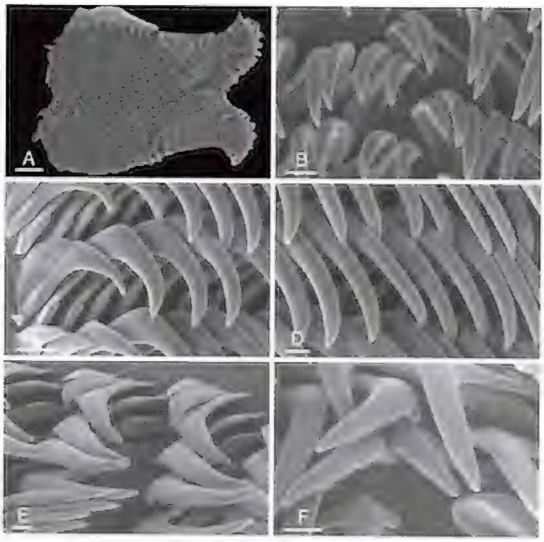

FIGURE 19. *Discodoris cebuensis*, radula. A. CASIZ 156672, scale = 200 µm.— B. Innermost teeth, CASIZ 156672, scale = 20 µm.— C. Outermost teeth, CASIZ 156672, scale = 40 µm.— D. Median teeth, CASIZ 156672, scale = 20 µm.— E. Outermost teeth teeth, CASIZ 110447, scale = 20 µm.— F. Innermost teeth, CASIZ 110447, scale = 20µm.

Nervous system. The circum-esophageal nerve ring is short, i.e., its length equals the dorsal width of the ganglia. The cerebral and pleural ganglia are fused, and more or less fused with the pedal ganglia.

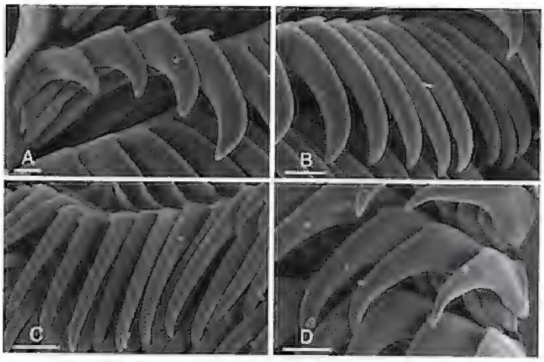

FIGURE 20. *Discodoris cebuensis*, radula. A. Outermost teeth, CASIZ 168013, scale = 20 µm.— B. Median teeth, CASIZ 168013, scale = 30 µm.— C. Median teeth, CASIZ 093937, scale = 40 µm.— D. Outermost teeth, CASIZ 093937, scale = 40 µm.

Reproductive system. The ampulla is straight or convoluted (from one to three loops). It enters immediately into the female gland mass. The division between male and female ducts cannot be seen by dissection. The prostate is divided in a proximal, whitish part, and a distal, yellowish part. Both parts are easily recognizable. The deferent duct is tightly convoluted. However, the number of loops varies (from just a few to many loops). No distal accessory gland and no distinct penial papilla were found. The vaginal duct is straight; the fertilization duct is convoluted (one or two loops). The disappearance of the fertilization duct into the female gland mass is not marked by a distinct duct. The size of the bursa copulatrix equals from one to two times the size of the receptaculum seminis. The two spermatic pouches are close to one another or clearly separated.

DIAGNOSTIC FEATURES.— The color pattern of the dorsal notum is a distinguishing feature, acknowledging that it can vary among individuals. In addition, anatomical features, such as the loops of the vas deferens, can be helpful, although they are not really diagnostic because several other species have convoluted deferent ducts, such as *boholiensis*. Tight hemispherical tubercles are found on the dorsal notum of preserved specimens, but they may be absent in live animals. The radula can hardly be distinguished from the radula of *boholiensis*, but the fragile notum of *boholiensis* is different from the notum of *cebuensis*. Therefore, radular teeth should only be used in combination with other features.

INFRA-SPECIFIC CHARACTER VARIATION.— The literature does not provide any significant, additional data on individual character variation.

DISCUSSION.— The fact that all specimens dissected for the present study and the holotype of *cebuensis* are part of the same species is supported by several features: the dorsal notum, especially the tight hemispherical tubercles, and the presence of several large, blue tubercles; the color described by Bergh for the preserved holotype of *cebuensis* is compatible with additional specimens examined here (note that the blue-purple large spots disappear with preservation); the radular teeth are exactly the same. A radula of a specimen of *cebuensis* could not be distinguished from the radula of a specimen of *boholiensis*. However, these two species have a distinct notum. The notum of *boholiensis* is fragile and thin, and cannot be mistaken with that of *cebuensis*. Eliot (1910a) identified two specimens from Coetivy Island, Seychelles, as *cebuensis*. Unfortunately, the features that he mentioned (1910a:424) are vague: one 35 mm long specimen was "almost pure white, with traces of brown color in the middle of the back," the other, 15 mm long, was "bluish white with many spots of various shades of purple," and with "a few brownish flecks on the undersides." The radular formulae were 20 × (30-0-30) and 17 × (20-0-20), and the innermost teeth had a "small denticle at the base of the shaft." All these features are compatible with *cebuensis* but they also are compatible with other species, especially *Peltodoris*

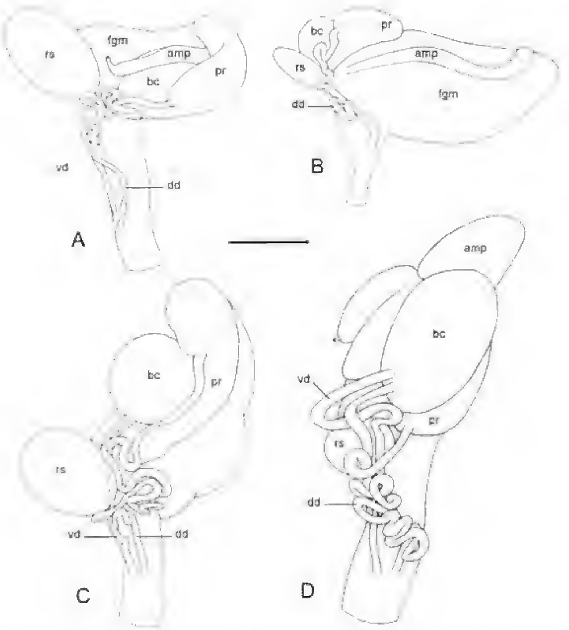

FIGURE 21. *Discodoris cebuensis*, reproductive system. A. CASIZ 156672, scale = 1 mm.— B. CASIZ 099355, scale = 2.5 mm.— C. CASIZ 070019, scale = 4 mm.— D. CASIZ 168013, scale = 0.65 mm.

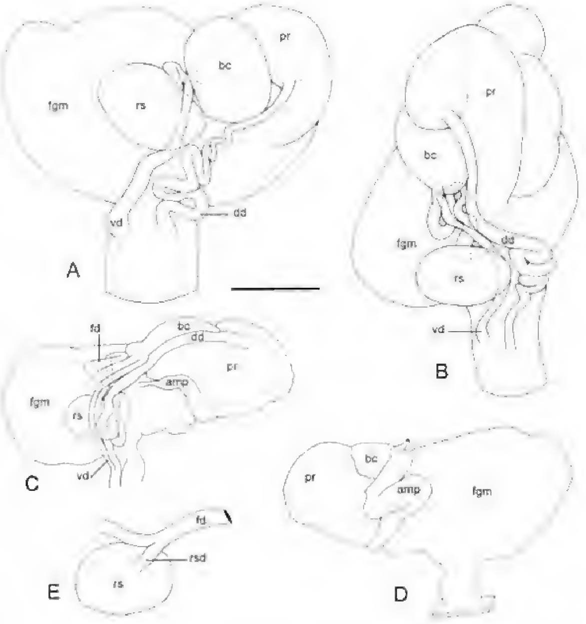

FIGURE 22. *Discodoris cebuensis*, reproductive system. A. CASIZ 070018, scale = 2 mm.— B. CASIZ 110447, scale = 2 mm.— C. CASIZ 110381, scale = 2.5 mm.— D. CASIZ 110381, scale = 2.5 mm.— E. CASIZ 110381, scale = 1 mm.

murrea (because of the "bluish white [color] with many spots of various shades of purple"). However, Eliot's identification is accepted because he examined the type material of *cebuensis*. Finally, an old specimen (not dissected here) is misidentified as *Discodoris cebuensis* in the ZMUC collection (it could belong to *Baptodoris*).

Eliot (1910a:422) pointed out that *schmeltziana* was "elaborately described" but that it did "not seem to have any certain characters except the color." In fact, several specimens with a dorsal color similar to the color illustrated in Garrett's drawings (Bergh 1880a:plate A, figs 15-19) were identified as *schmeltziana* (Dayrat and Gosliner 2005; see also, Bill Rudman's *Sea Slug Forum*, fact sheet of *Discodoris schmeltziana*). The similarity is striking. Unfortunately, Bergh's (1880a) re-description of *schmeltziana*, was based on two specimens, and it is likely that the specimen illustrated in Bergh (1880a) was not the holotype, by monotypy, from the original description (Bergh 1875). Therefore, the name *schmeltziana* should not be used as the valid name for *cebuensis* and is regarded here as a *nomen dubium*.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *cebuensis* shows that it is nested with two other species (*boholiensis* and an unnamed species described here, sp. A) within a clade. Because *boholiensis* is the type species of *Discodoris*, this clade can reasonably be called *Discodoris*. The Linnaean binomial for *cebuensis* should be *Discodoris cebuensis*, which is also a possible name under the *ICPN*.

***Discodoris* sp. A new, unnamed species**

Figures 23-26.

MATERIAL DISSECTED.— **Japan**, Ryukyu Islands, Okinawa, Seragaki Tombs, 1.3 km ENE Maekizaki, Seragaki Beach, 26°30.40′N, 127°52.60′E, 3 meters depth, 9 January 1993, one specimen 23/15 mm preserved, leg. Robert F. Bolland, identified as *Discodoris* by T. M. Gosliner (CASIZ 089040).

MATERIAL EXAMINED (NOT DISSECTED).— **Japan**, Ryukyu Islands, Okinawa, Seragaki Tombs, 1.3 km ENE Maeki-zaki, 26°30.40′N, 127°52.60′E, 3 meters depth, 4 April 1995, one specimen 16/8 mm preserved, leg. Robert F. Bolland, identified as *Discodoris* by T. M. Gosliner (CASIZ 105315).

DISTRIBUTION.— Japan (Okinawa).

HABITAT.— Found attached to lower surface of slab of coral rubble as it was overturned (CASIZ 105315), on mixed sand coral rubble in reef (CASIZ 089040).

DESCRIPTION OF NEW SPECIMENS (Figs 23-26).— *Color.* The ground color of the dorsal notum is reddish-orange but is abundantly mottled with white, dark red, and brown areas. In particular, there are a few larger tubercles that are white and around which smaller tubercles are white as well. Those larger tubercles are arranged in two longitudinal rows of four to five larger tubercles on either side of the median line between the rhinophores and the gills. The edge of the notum is darker (reddish, blackish) than the rest of the notum, but a thin white line runs all around the margin of the notum. Also, a few white tubercles are randomly located on the lateral wing of the dorsal notum: those tubercles are not as large as the ones arranged in the two longitudinal rows, but they tend to be larger than the rest of the tubercles. The foot of the rhinophores is creamish but the lamellae are black, although their edges can be white. The branchial plumes are black with white margins. I ignore the ventral color of live animals. Preserved animals have a creamish ventral ground color with red-brown dots, and a light red-brown dorsal ground color, at least in the median part because the lateral wing is more creamish.

External morphology. The body is oval. Its length equals less than twice its width. The dorsal notum bears tubercles that are not caryophyllidia. They are all more or less of the same size, except for a few that are larger (and white): those are arranged in two longitudinal rows on either side of the median line. Some larger tubercles are also randomly arranged on the lateral wing of the dor-

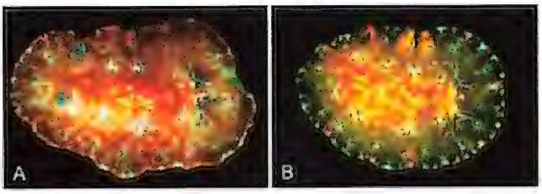

FIGURE 23. *Discodoris* sp. A, dorsal color. A. CASIZ 089040 (R.F. Bolland).— B. CASIZ 105315 (R.F. Bolland).

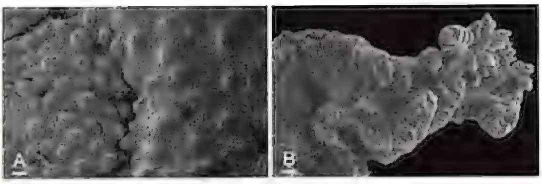

FIGURE 24. *Discodoris* sp. A, CASIZ 089040. A. Dorsal notum, tubercles, scale = 200 μm.— B. Branchial plume, scale = 100 μm.

sal notum. Small holes (diameter < 10 μm) and many small tufts of cilia were found on the mantle, including the dorsal tubercles, the oral tentacles, the rhinophores and the gills. The foot is rounded posteriorly and anteriorly. The anterior foot is bilabiate and the upper lip is notched. The oral tentacles are digitiform, not grooved. There are six tripinnate branchial plumes. The rhinophores have from 15 to 20 lamellae.

Digestive system. The stomach is not free. It is largely embedded within the digestive gland. The intestine is straight and dorsal. The labial cuticle is armed with a pair of jaw plates. The jaws are two narrow bands of a few rows of rodlets (maximum ten rows). The jaw plates are not strong and sickle-shaped. The rodlet tips are irregular. The length of the radula equals about twice its width. The radular sac cannot be seen by dorsal dissection. The radular formula of the 23 mm long individual is 28 × (37-0-37). The rachidian teeth are absent and the rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the teeth gradually increases from the first innermost tooth up to the tenth lateral tooth, then stays approximately constant, and finally decreases for the last five or seven outermost teeth. The last two outermost teeth are reduced, and often just triangular, not hamate. The tooth hooks are significantly thinner and more elongated than in other species studied here. The teeth bear no outer denticles, except for the outermost tooth that bears five to eight short denticles on the margin. The tooth foot has a wing on its inner, anterior edge. This wing can only be seen if a tooth is observed on its inner lateral view. In dorsal view, it appears as a spur on the inner edge of the tooth hooks.

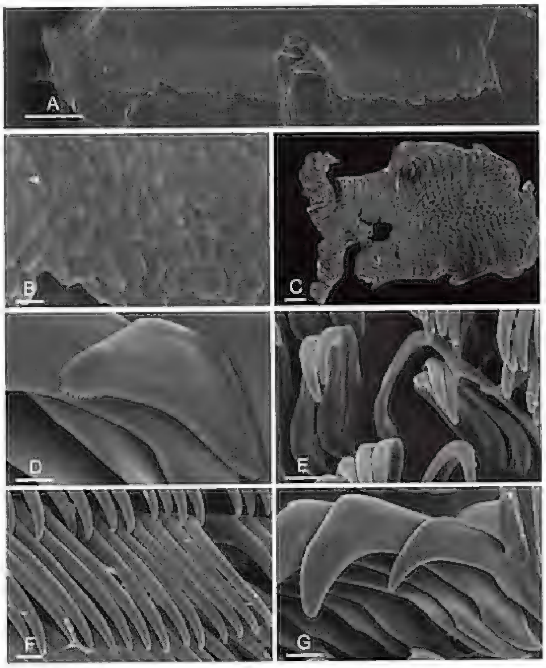

FIGURE 25. *Discodoris* sp. A, CASIZ 089040. A. Two lateral jaws, scale = 100 μm.— B. Jaw rodlets, scale = 10 μm.— C. Radula, scale = 200 μm.— D. Outermost teeth, scale = 10 μm.— E. Innermost teeth, scale = 20 μm.— F. Median teeth, scale = 20 μm.; G. Outermost teeth, scale = 20 μm.

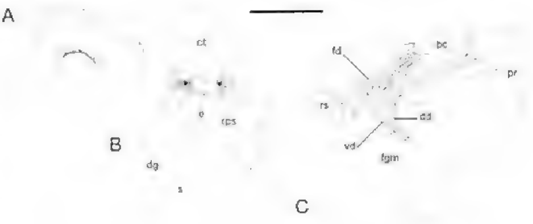

FIGURE 26. *Discodoris* sp. A, CASIZ 089040. A. Anterior, ventral view, total width = 12 mm.— B. Anterior, internal general anatomy, scale = 8 mm.— C. Reproductive system, scale = 4 mm.

Nervous system. The circum-esophageal nerve ring is short; its length equals approximately twice the width of the dorsal ganglia. The cerebral and pleural ganglia are fused.

Reproductive system. The ampulla is loosely convoluted. The division between male and female ducts could not be seen by dissection. The prostate is divided in a proximal whitish part and a distal yellowish part. The deferent duct is straight. A papilla was found at the distal end of the deferent duct, but it does not seem to be a distinct penis. No distal accessory gland was found. The vaginal duct is convoluted (a few loose loops). The fertilization duct is straight. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is marked by a short duct. The ovate bursa copulatrix is about twice as large as the spherical receptaculum seminis. The spermatic pouches are not attached.

DISCUSSION.— Those two specimens likely are part of a new, unnamed species. They share many characteristics with *boholiensis* and *cebuensis* (e.g., distinct lateral teeth, with a long, narrow hook). However, they also differ from *boholiensis* and *cebuensis* for several features, such as the dorsal color, the radular anatomy (outermost tooth with marginal denticles), and the genital anatomy (e.g., length of deferent duct). Therefore, although those two specimens here are closely related to *boholiensis* and *cebuensis*, they are part of a new species. I have decided to wait to name it because I need more specimens to evaluate the infra-specific variation of the diagnostic features.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of sp. A shows that it is nested with two other species (*boholiensis* and *cebuensis*) in the clade *Discodoris*. Sp. A should be referred to as *Discodoris* sp. A.

Peltodoris Bergh, 1880

Under the *ICZN*, *Peltodoris* is a taxon of genus-level. Type-species: *Peltodoris atromaculata* Bergh, 1880, by subsequent designation by O'Donoghue (1929:766).

The phylogenetic diagnosis of *Peltodoris* includes three classes of characters, depending on their phylogenetic significance. 1) One synapomorphy exclusively found in this taxon: 10 to 15 innermost teeth significantly smaller than the rest of the lateral teeth; only this synapomoraphy can be regarded as diagnostic of *Peltodoris* (i.e., only this character can be used to identify that a species belongs to *Peltodoris*). 2) Four synapomorphies of *Discodorididae*: a notched upper lip of the bilabiate anterior foot, digitiform or conical oral tentacles that are *not* expansions of the lateral mouth lips, a flattened prostate divided in two parts of distinct color, and two blood glands. 3) Characters found in many other dorid nudibranchs, e.g., absence of rachidian teeth, hamate lateral teeth, etc.

In the present contribution, *Peltodoris* refers to a clade name, without being assigned to any particular rank. Under the *ICPN*, *Peltodoris* is a converted clade name: it remains an informal clade name until it is phylogenetically defined *and* formally registered. *Peltodoris* could be phylogenetically defined through an apomorphy-based definition as "the clade stemming from the first organism or species to possess a radula with 10 to 15 innermost teeth significantly smaller than the rest of the lateral teeth as inherited by *Peltodoris atromaculata* Bergh, 1880."

Peltodoris atromaculata Bergh, 1880

Figures 27-35.

Peltodoris atromaculata Bergh, 1880a:41, 45-46.— Bergh, 1880b:222-232, plate XI, figs 1-15.— Carus, 1893:219.— Vayssière, 1913:323 [erroneous authorship as *atromaculata* Risso, 1826].— O'Donoghue, 1929:766.— Pruvot-Fol, 1951:10.— Pruvot-Fol, 1954a:242, fig. 91.— Sordi and Majidi, 1955:239.— Changeux and Debouteville, 1955:289.— Wirz-Mangold and Wyss 1958:36.— Haefelfinger, 1960:335.— Haefelfinger, 1961:331-343, figs 1-7.— Vicente, 1964:222.— Vicente, 1967:150, 163, 167, plate 1, fig.

4.— Fournier, 1969:73-93, figs a-e.— Schmekel, 1968:115.— Sordi 1970:110.— Starmühlner, 1968:16.— Starmühlner, 1969:227.— Schmekel, 1970:195-196, fig. 57a.— Nordsieck, 1972:63.— Ros, 1975:329-330.— Barash and Danin, 1971:179.— Ros, 1976a:46, 48, fig. 1A.— Ros, 1976b:36.— Ros and Altimira, 1977:48.— Castiello et al., 1979:5047-5050.— Castiello et al., 1980:413-416.— Perrone, 1980:121-127, figs 2-3.— Altimira et al., 1981:73.— Bibiloni, 1981:45, 48.— Templado, 1982:251.— Barash and Danin, 1982:102.— Schmekel and Portmann, 1982:86-87, fig. 7.16, plate 3, fig. 1, plate 20, fig. 11.— Garcia Gomez, 1983:43.— Riedl, 1983:337, plate VII, plate 117.— Jonas, 1985:298-310.— Jonas, 1986:207-216.— Ros, 1985a:91.— Ros, 1985b:125.— Thompson, 1985:222-226, figs 1-2.— Ballesteros et al., 1986:51.— Ortea and Flor, 1986:61, unnumbered figure.— Perrone, 1986:37.— Marin and Ros, 1987:141.— Barash and Danin, 1988:57.— Barash and Danin, 1989:255, fig. 8.— Perrone, 1989:187-188.— Bello, 1989:363-366.— Perrone, 1992:81-84, figs 1-3.— Pérez and Moreno, 1991:234, unnumbered figure.— Barash and Danin, 1992:214-215.— Avila, 1996:151-157, fig. 1.— Avila and Durfort, 1996:149-150, 157, 160, fig. 14.— Cattaneo-Vietti et al., 2001:77-80.— Valdés, 2002:585-586, figs 4H, 28, 29.

Peltadoris tuberculata (Cuvier).— Demetropoulos, 1969:14 [possible spelling mistakes; accepted as a record of *Peltodoris atromaculata* by Barash and Danin (1989)].

Discodoris atromaculata.— Cervera et al., 1988:35.— Cattaneo-Vietti et al., 1990:82-83, plate 5, fig. 4.— Cattaneo-Vietti et al., 1993:173-180, fig. 1.— Koutsoubas and Koukouras, 1993:196.— Wirtz and Martins, 1993:56-57.— Wirtz, 1995:178-179, unnumbered figure.— Wirtz, 1998:9, plate 4, fig. 2.— Wirtz, 1999:12-13.— Malaquias et al., 2001:78.— Gavaia et al., 2003:111-112, plate I, fig. F.— Trainito, 2003:34-35, figs 85-90.

Discodorididae atromaculata.— Dayrat and Gosliner, 2005:205.

TYPE MATERIAL.— Holotype (ZMUC GAS-2054), by monotypy: one specimen 34/20 mm preserved [46/25 mm alive], leg. Dr. Dohrn, May 1880. It is worth pointing out that *atromaculata* was described twice as a new species, in two different contributions published by Bergh in 1880. However, the fact that Bergh (1880a:41) mentions that the description of *atromaculata* will be provided in the *Mittheilungen aus der Zoologischen Station in Neapel* strongly suggests that Bergh's (1880a) contribution was the first to be published.

TYPE LOCALITY.— Zoological Station, Naples, [Mediterranean].

TYPE MATERIAL CONDITION.— The holotype was dissected by Bergh. Only the body wall, the digestive gland, and the six tripinnate branchial plumes are present in the jar. The dorsal color is well preserved.

ADDITIONAL MATERIAL DISSECTED.— **Mediterranean Sea**, Spain, Granada, La Henadura, 31 March 1983, one specimen 20/12 mm preserved, leg. A. Luque, identified as *Peltodoris atromaculata*, [identifier unknown, probably A. Luque], (MNCN 15.05/1.984); Mediterranean Sea, Spain, Murcia, Cabo de Palos, [collecting date unknown], two specimens 60/50 (#1) and 36/22 (#2) mm preserved, leg. J. Templado, identified as *Peltodoris atromaculata*, [identifier unknown, probably J. Templado], (MNCN 15.05/18240); Mediterranean Sea, Spain, Murcia, Cabo de Palos, 13 October 1988, two specimens 55/40 (#1) and 50/40 (#2) mm preserved, leg. J. Templado and M. Calvo, identified as *Peltodoris atromaculata*, [identifier unknown, probably J. Templado and M. Calvo], (MNCN 15.05/18243); Mediterranean Sea, Spain, Murcia, Cabo de Palos, Bajo de Enmedio, 2 August 1984, one specimen 60/40, leg. J. Templado, identified as *Peltodoris atromaculata*, [identifier unknown, probably J. Templado], (MNCN 15.05/18242); Mediterranean Sea, Spain, Mallorca, Cabo Menorca, 39°53.00′N, 03°11.80′E, 22 meters maximum depth, 26 June 1994, one specimen 45/35 mm preserved, leg. Field expedition FAUNA III 191 B_5, identified as *Peltodoris atromaculata* by J. Templado (MNCN 15.05/19.326); Mediterranean Sea, Spain, Mallorca, 39°45.55′N, 02°37.50′E, 25 meters maximum depth, 25 June 1994, one specimen 50/35 mm preserved, leg. Field expedition FAUNA III 185 B_5, identified as *Peltodoris atromaculata* by J. Templado (MNCN 15.05/19.336); **Atlantic Ocean**, Portugal, Sagres, Punta de Baleeira, 23 June 2001, one specimen 35/25 mm preserved, [leg. Gavaia et al. 2001], identified as *Peltodoris atromaculata* [by Gavaia et al. 2001], (MNCN 15.05/46485) [voucher: Gavaia et al. 2001]; Atlantic Ocean, Azores, Ilha Saõ Miguel, 1 km East of Caloura, 20 July 1988, one specimen 50/40 mm preserved, leg

T. M. Gosliner and J. Brum, identified as *Peltodoris atromaculata* by T. M. Gosliner (CASIZ 072584) [this lot includes several other specimens].

DISTRIBUTION.— Mediterranean Sea and eastern Atlantic Ocean: Aegean Sea (Koutsoubas and Koukouras 1993), Rhodes (Barash and Danin 1988), Cyprus (Demetropoulos 1969; Barash and Danin 1989), Israel (Barash and Danin 1971, 1992), Alexandria (Steuer 1939, cited in Barash and Danin 1971), Malta (Barash and Danin 1992), Italy (Bergh 1880a, 1880b; Sordi and Majidi 1955; Schmekel 1970; Schmekel and Portmann 1982; Cattaneo-Vietti et al. 1990; Perrone 1992; Cattaneo-Vietti et al. 1993), Mediterranean coasts of France (Pruvot-Fol 1954a; Changeux and Delamare Deboutteville, 1955; Haefelfinger 1960, 1961; Vicente 1967; Fournier 1969), Mediterranean coasts of Spain (Cervera et al. 1988, and references therein; present study), Gibraltar Strait (Garcia Gomez 1983), Asturias, Atlantic coasts of Spain (Ros 1975; Ortea and Flor 1986), coasts of Portugal (Gavaia et al. 2001; present study), Canary Islands (Pérez and Moreno 1991), Azores (Wirtz 1998; present study), Madeira (Wirtz 1999; Malaquias et al. 2001).

HABITAT.— Several studies (e.g., Haefelfinger 1961; Fournier 1969; Ros 1975; Castiello et al. 1979) have shown that *atromaculata* is associated with the sponge *Petrosia*, on which it preys. It is found from the intertidal zone up to 52 meters (Vicente 1964) or 80 meters (Barash and Danin 1992) depth. Many specimens have been collected in shaded sea caves or crevices.

OCCURENCE.— Common in western Mediterranean (e.g., Vicente 1964; Cattaneo-Vietti et al. 1990), less common in eastern Mediterranean (Barash and Danin 1992).

LITERATURE.— Carus (1893), Vayssière's (1913), and O'Donoghue (1929) simply mentioned the presence of *atromaculata* in the Mediterranean based on Bergh's (1880a, 1880b) work. It seems that Pruvot-Fol (1954a) was the first who provided new records on the French coast of the Mediterranean. Most contributions that cite *atromaculata* provide distribution records with no additional data (e.g., Changeux and Delamare Deboutteville 1955; Sordi and Majidi 1955; Haefelfinger 1961; Templado, 1982; Ballesteros et al. 1986; Ortea and Flor 1986; Barash and Danin 1988, 1989, 1992). Many pictures of live animals have been published (e.g., Haefelfinger 1961; Vicente 1967; Perrone 1980; Ortea and Flor 1986; Barash and Danin 1989; Pérez and Moreno 1991; Avila 1996; Gavaia et al. 2001; Valdés 2002; Trainito 2003). Several features of *atromaculata* have been studied in great detail, such as mantle anatomy (Haefelfinger 1961; Avila and Durfort 1996), mantle chemistry (Castiello et al. 1979, 1980; Avila 1996 and references therein), variation of the color pattern (Thompson, 1985; Perrone 1989; Avila 1996), mantle autotomy and regeneration (Perrone 1992), mantle growth (Avila 1996), histology of the digestive system (Fournier 1969), stomach content (Cattaneo-Vietti et al. 1993), and gill epithelia (Jonas 1985, 1986). However, descriptions of some basic anatomical features, such as the radular teeth or the reproductive system, are rare (Bergh 1880b; Schmekel 1970; Schmekel and Portmann 1982; Cattaneo-Vietti et al. 1990; Valdés 2002). More importantly, the individual variation of those features has never been addressed, except for Cattaneo-Vietti et al. (1990) who provided a range of variation for the radular formula. Pruvot-Fol's (1954a) drawings and radular formula —20 × (56-0-56)— are from Bergh's (1880b).

WWW.— All the pictures of *atromaculata* posted on the *www* (both as *Discodoris atromaculata* and *Peltodoris atromaculata*) confirm the darkening of the notum along a cline from western to eastern Mediterranean (Thompson 1985): specimens from eastern Mediterranean have dark brown patches that are significantly larger than the specimens from western Mediterranean. In fact, some specimens from eastern Mediterranean are almost completely brown, with no white background left. The significance of this trend still is unknown.

REMARKS ON THE ORIGINAL DESCRIPTION.— These remarks deal with Bergh's (1880b) anatomical description of *atromaculata*, which is not the original description (see above), but is more thorough. Bergh (1880b) anatomical description of *atromaculata* is largely complete and, compared to his average descriptions, rich in illustrations (in particular, Bergh rarely drew the reproductive system). Bergh (1880b:225, fig. 1) carefully described the color of the live animal (46/25 mm) for which he obtained a drawing from Dr. A. Andres, present at the Zoological Station of Naples, and who like saw live animals. Also, the color of the live animal described by Bergh is well preserved: currently, the dorsal ground color of the holotype is whitish, including the gills and the rhinophores, with dark brown, round patches of various sizes; large patches are in the median part of the dorsal notum. The ventral surface is homogeneously whitish. Several morphological features described by Bergh were checked on the holotype: a bilabiate anterior foot with a notched upper lip, digitiform oral tentacles, semi-spherical and conical tubercles on the dorsal notum, six tripinnate branchial plumes. Bergh mentioned several other features, such as, twenty-two rhinophoral lamellae, a smooth labial cuticle, a radular formula of 20 × (55/56-0-55/56), hamate teeth with no denticles. Concerning the radula, a character has some phylogenetic significance (Fig. 30B): the innermost lateral teeth are significantly smaller than the rest of the lateral teeth (also the base of those innermost teeth bears a small spur). Bergh's original description of the reproductive system is informative: the prostate is flattened; the size of the spherical bursa copulatrix ('Spermatotheke') equals about three times the size of the pear-shaped receptaculum seminis ('Spermatocyste'); there is no distinct penis; the vaginal duct is smooth.

DESCRIPTION OF NEW SPECIMENS (Figs. 27-35).— *Color*. All preserved animals have the same color: a whitish background, including rhinophores and gills, with dark brown, regularly round patches of various sizes; the hyponotum and the pedal sole are whitish. Dark brown patches are largely faded (though still distinguishable) in CASIZ 072584, probably due to preservation.

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The width of the foot equals approximately one half of the width of the dorsal notum (in preserved specimens). The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform and not grooved. The dorsal notum bears tubercles that are not caryophillidia. In well-preserved nota, spicules almost do not come out from the tubercles; also, tubercles have a fully ciliated apex. Small holes (diameter < 10 μm) and many small tufts of cilia were found on the mantle, including the rhinophores and the gills. In preserved specimens, the margins of the rhinophoral and branchial sheaths can be smooth or lightly crenulate. There are six bipinnate (MNCN 15.05/1.984, MNCN 15.05/19.336) or tripinnate branchial plumes. The rhinophores have from sixteen to thirty lamellae (but usually from twenty to twenty-five), depending on the size of the animals. Two specimens (MNCN 15.05/18243 and MNCN 15.05/18240) have a thin muscular layer under the mantle, as in *fragilis* (see this species).

Digestive system. The stomach is large, free, on top of the left anterior side of the digestive gland. A caecum is present. The intestine is straight and dorsal. The labial cuticle is unarmed. The radular sac cannot be seen by dorsal dissection. The radular formulae are: 17 × (35-0-35) in a 20 mm long specimen (MNCN 15.05/1.984), 17 × (45-0-45) in a 45 mm long specimen (MNCN 15.05/19.326), 18 × (45-0-45) in a 50 mm long specimen (CASIZ 072584), 19 × (40-0-40) in a 50 mm long specimen (MNCN 15.05/19.336), 19 × (40/45-0-40/45) in a 55 mm long specimen (MNCN 15.05/18243 #1), 20 × (40-0-40) in a 60 mm long specimen (MNCN 15.05/18240 #1), 20 × (45/50-0-45/50) in a 35 mm long specimen (MNCN 15.05/46485), 20 × (40-0-40) in a 60 mm long specimen (MNCN 15.05/18242), 23 × (40/45-0-40/45) in a 45 mm long specimen (MNCN 15.05/18243 #2), 26 × (56-0-56) in a 36 mm long specimen (MNCN 15.05/18240 #2). The radular formula is not strictly correlated to the size of the preserved animals. Rachidian teeth are absent. The median area of the radula bears approximately ten innermost lateral teeth that are significantly smaller than the rest of the lateral teeth. The width of this median area equals one third of the total width of the radula. The small, innermost teeth are only present in the anterior (i.e., the oldest) half of the radula. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the innermost teeth that are significantly smaller and the last three or four outermost ones of which the size decreases gradually; the outermost tooth can be vestigial. All teeth are hamate and not grooved; they bear no denticles. However, the base of the innermost teeth bears a spur of which the size varies and that may be absent too.

Nervous system. The circum-esophageal nerve ring is short. The cerebral, pleural, and pedal ganglia are more or less fused. They are distinguishable (e.g., CASIZ 072584) or undistinguishable (MNCN 15.05/18243). The surface of the ganglia is smooth, although some spherical masses can be seen through the surface.

Reproductive system. The ampulla is loosely convoluted (one or two loops) before reaching the female gland mass. The division between male and female ducts (hidden within the female gland mass) could not be seen by dissection. The flattened prostate is divided in two parts, a proximal whitish part and a distal yellowish part. The deferent duct is loosely convoluted. No distinct copulatory organ is present: a papilla was found in one specimen (e.g., MNCN 15.05/19.326), which certainly is the evaginable, distal part of the deferent duct. The vaginal duct is straight. No accessory gland is present. The fertilization duct is loosely convoluted near the bursa copulatrix. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is marked by a distinct duct. The size of the bursa copulatrix equals from two (e.g., MNCN 15.05/18242) to ten (MNCN 15.05/19.326) times the size of the receptaculum seminis. Both pouches are spherical-ovate. The surface of the bursa copulatrix is smooth; the surface of the receptaculum seminis is smooth (e.g., MNCN 15.05/46485) or covered with small granular protuberances (e.g., MNCN 15.05/18240 #1).

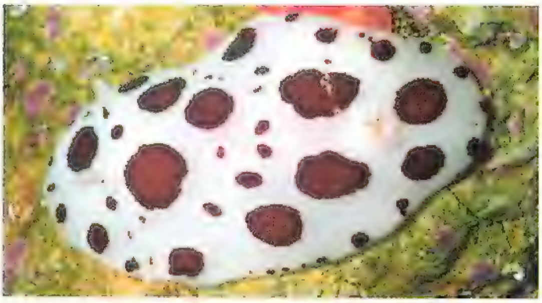

FIGURE 27. *Peltodoris atromaculata*, dorsal color. CASIZ 099147 (Spain, Gerona, Illes Medes, one of three specimens).

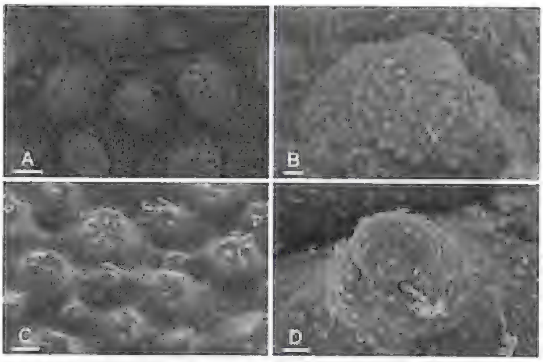

FIGURE 28. *Peltodoris atromaculata*, dorsal notum, tubercles. A. MNCN 15.05/18240 (#1), scale = 100 µm.— B. MNCN 15.05/18240 (#1), scale = 20 µm.— C. MNCN 15.05/46485, scale = 100 µm.— D. MNCN 15.05/46485, scale = 20 µm.

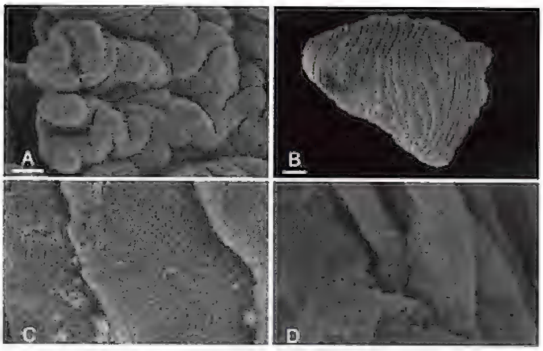

FIGURE 29. *Peltodoris atromaculata*. A. Branchial plumes, CASIZ 072584, scale = 60 µm.— B. Rhinophore, MNCN 15.05/18240 (#2), scale = 200 µm.— C. Rhinophoral lamellae, MNCN 15.05/18240 (#2), scale = 40 µm.— D. Branchial plume (detail), MNCN 15.05/18240 (#1), scale = 20 µm.

DIAGNOSTIC FEATURE.— The diagnostic feature of *atromaculata* is the color of the dorsal notum.

Infra-specific variation.— The size of the specimens dissected for the present study is compatible with the sizes usually cited in the literature. The largest specimens dissected here (MNCN 15.05/18240 #1, MNCN 15.05/18242) are 60 mm long preserved, i.e., about 80/90 mm alive. The maximum sizes found in the literature are 75 mm (Ros 1975; Pérez and Moreno 1991), 120 mm (Schmekel and Portmann 1982), and 150 mm (Cattaneo-Vietti et al. 1990). There is no significant trend in size variation from eastern Atlantic to eastern Mediterranean. Cattaneo-Vietti et al. (1990) have mentioned the presence of eight branchial plumes instead of six. Authors have mentioned 20 to 25 (Cattaneo-Vietti et al. 1990), 22 (Valdés 2002), and 25 (Schmekel and Portmann 1982) rhinophoral lamellae. The broader range of variation observed here (from 16 to 30 lamellae) is explained by the fact that specimens of different sizes were dissected. The radular formulae mentioned here also are compatible with the literature: 16 × (38-0-38) in a 40 mm long specimen and 18 × (52-0-52) in a 90 mm long specimen by

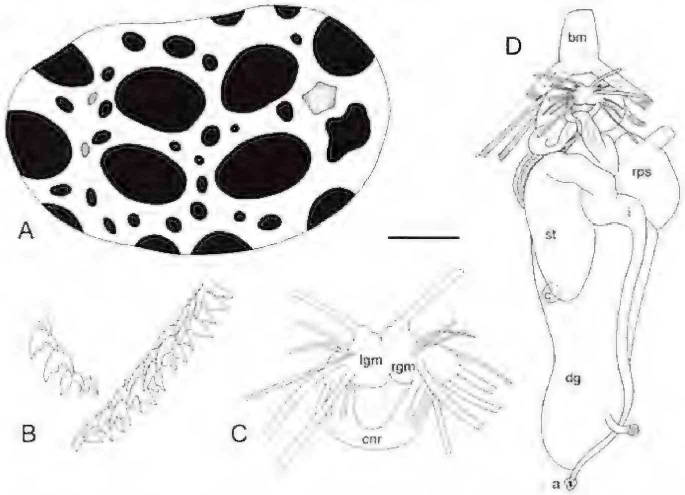

Figure 30. *Peltodoris atromaculata*. A. Holotype, dorsal view (as currently preserved), total length = 34 mm.— B. Innermost teeth, after Bergh (1880b: fig. 3).— C. Nervous system, CASIZ 072584, scale = 2 mm.— D. General anatomy, CASIZ 072584, scale = 7.5 mm.

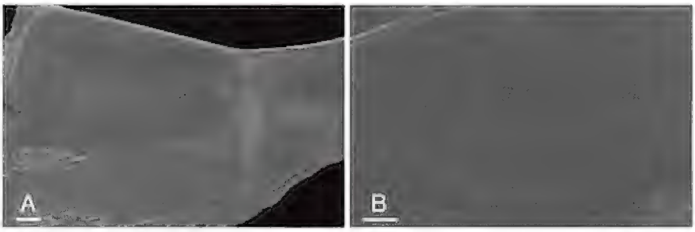

Figure 31. *Peltodoris atromaculata*, smooth labial cuticle. A. MNCN 15.05/46485, scale = 100 µm.— B. Labial cuticle, detail, MNCN 15.05/46485, scale = 40 µm.

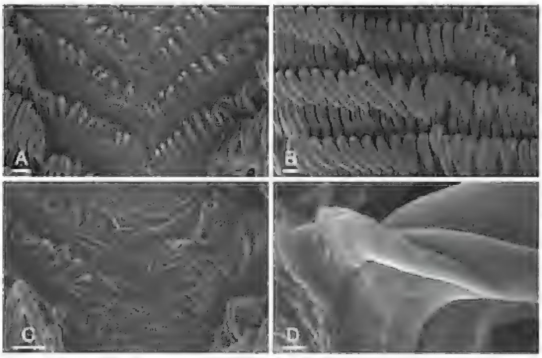

Figure 32. *Peltodoris atromaculata*. A. Radula, innermost teeth, CASIZ 072584, scale = 100 µm.— B. Radula, median teeth, CASIZ 072584, scale = 100 µm.— C. Radula, innermost teeth, MNCN 15.05/19.326, scale = 100 µm.— D. Radula, outermost tooth, MNCN 15.05/1.984, scale = 5 µm.

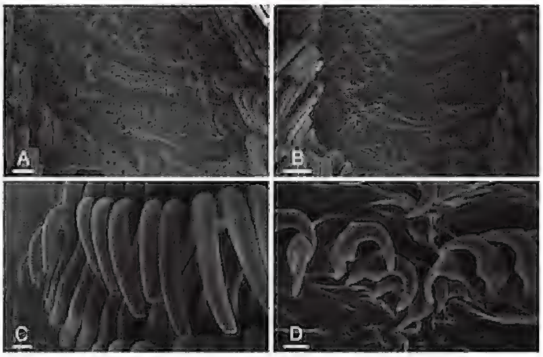

Figure 33. *Peltodoris atromaculata*. A. Radula, innermost teeth, MNCN 15.05/18240 (#2), scale = 100 µm.— B. Radula, innermost teeth, MNCN 15.05/19.336, scale = 100 µm.— C. Radula, innermost teeth, MNCN 15.05/19.336, scale = 30 µm.— D. Radula, outermost teeth, MNCN 15.05/19.336, scale = 20 µm.

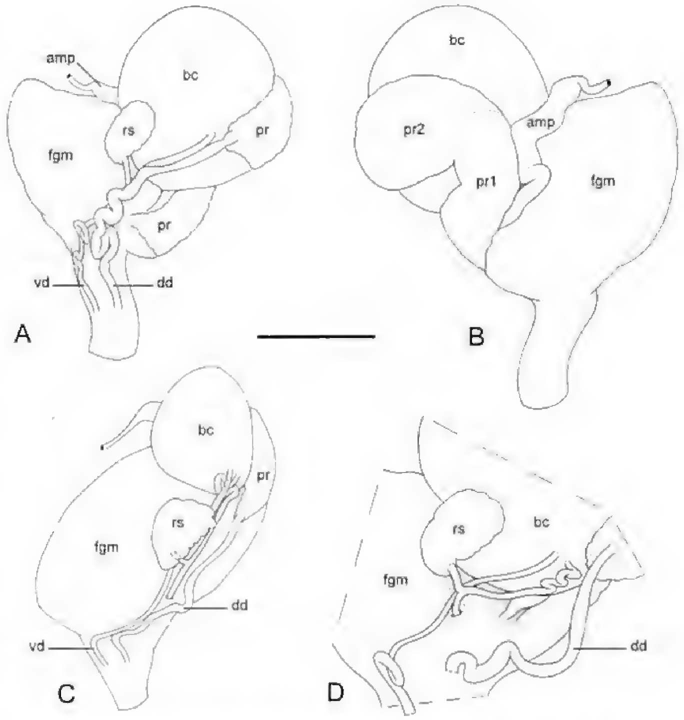

FIGURE 34. *Peltodoris atromaculata*, reproductive system. A. CASIZ 072584, scale = 4.3 mm.— B. CASIZ 072584, scale = 3.3 mm.— C. MNCN 15.05/18240 (#1), scale = 4 mm.— D. Spermatic ducts (receptaculum seminis was moved), CASIZ 072584, scale = 3.9 mm.

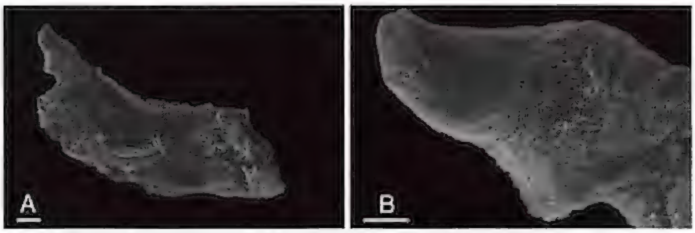

FIGURE 35. *Peltodoris atromaculata*. A. Penial papilla, with connective tissue surrounding the distal deferent duct, MNCN 15.05/19.326, scale = 100 µm.— B. Penial papilla, MNCN 15.05/19.326, scale = 30 µm.

Schmekel and Portmann (1982), 14/20 × (35/50-0-35/50) by Cattaneo-Vietti et al. (1990), and 22 × (48-0-48) in a 54 mm long specimen by Valdés (2002). In summary, the maximum number of radular rows is 26 (present study), and the maximum number of lateral teeth is 56 (Bergh 1880b; present study). Finally, Valdés's (2002) description of the reproductive system (e.g., bursa copulatrix ten times as large as the receptaculum seminis), based on a single specimen, does not reflect the actual individual variation found in *atromaculata* (see above).

DISCUSSION.— The identification of *atromaculata* has never been problematic. Cattaneo-Vietti and co-authors (1990) rightly consider that *atromaculata* is "unmistakable." As a matter of fact, it has never been misidentified. The only issue has been whether it should be placed within *Peltodoris* or *Discodoris*.

SUPRA-SPECIFIC RELATIONSHIPS.— Several authors (e.g., Cervera et al. 1988; Cattaneo-Vietti et al. 1990) have used the combination *Discodoris atromaculata* without explanation (although, likely, because of Thompson's synonymy between *Peltodoris* and *Discodoris*, based on the idea that the absence/presence of jaws on the labial cuticle was an arbitrary criterion to separate *Peltodoris* from *Discodoris*). In any case, *atromaculata* is nested with two other species (*mullineri*, *murrea*) in a clade supported by the presence of median area of the radula with approximately 10 to 15 innermost lateral teeth that are significantly smaller than the rest of the lateral teeth). Because *atromaculata* is the type species of *Peltodoris* under the *ICZN*, it makes sense to call this clade *Peltodoris*. Therefore, the Linnaean binomial should remain *Peltodoris atromaculata*, which also is a possible name under the *ICPN*.

FUTURE STUDIES.— A potentially interesting research would be to evaluate the genetic diversity and the amount of gene flow that exist between populations from eastern Atlantic and eastern Mediterranean. Also, it would be interesting to compare this population structure with the population structure of the sponges with which *atromaculata* is associated. Broadly speaking, it would be interesting to address the causes for the East-West trend observed for the color (eastern individuals are much darker).

Peltodoris mullineri **Millen and Bertsch, 2000**

Figures 36-38.

Peltodoris mullineri Millen and Bertsch, 2000:357-361, figs 1B, 4-5.— Behrens and Hermosillo, 2005:75, fig. 143.
Peltodoris sp. 1. Behrens, 1991:69, fig. 124.

Type material.— Holotype (CASIZ 074262), by original designation: one specimen 35/25 mm preserved, leg. T. M. Gosliner, 19 October 1985. Two paratypes: one specimen 45/35 mm preserved, leg. D. W. Behrens, 14 December 1979 (CASIZ 069302); one specimen 40/35 mm preserved, leg. R. Van Syoc, 23 August 1984 (CASIZ 074651).

Type locality.— Holotype: Isthmus Cove, Santa Catalina Island, Channel Islands, California. The localities of the paratypes are: Fisherman's Cove, Catalina Island, Channel Islands, California (CASIZ 069302); Santa Cruz Island, Channel Islands, California (CASIZ 074651).

Type material condition.— The holotype was not dissected. The paratypes were entirely dissected by Millen and Bertsch: the buccal mass (including the labial cuticle) is missing in one paratype (CASIZ 074651); the reproductive system is largely destroyed in the other paratype (CASIZ 069302); pieces of the notum of both paratypes for SEM were prepared here; the reproductive system of one paratype (CASIZ 074651) is illustrated here as well.

Distribution.— This species is known from the Channel Islands, the Gulf of California (Behrens 2004), and Isla de Malpelo, Columbia (Behrens and Hermosillo 2005).

Habitat.— Large boulders and overhangs (CASIZ 074651).

Remarks on the original description (Figs. 36-38).— The original description of *mullineri* is largely complete: a color picture of a live animal, several SEM pictures, and an informative drawing of the reproductive system are provided. A few features are emphasized. The maximum size of live animals is 70 mm in length (and 45 mm, preserved). The body is slightly flattened, and its texture is rigid. The color of live animals vary from "pale cream to bright yellow to golden orange (…) with dark brown, speckled blotches, which are formed by clusters of tubercles having dark pigments at their bases and ides, but retaining light tips." The dorsal ground color is currently whitish in the paratypes and slightly yellowish in the holotype. However, the dark blotches remain (although they are lighter due to preservation). The hyponotum and the foot are currently whitish in the holotype; they bear additional dots and spots in the paratypes. The oral tentacles are digitiform and not grooved. The anterior foot is bilabiate, with the superior lip notched. Rhinophores consist of about 25 lamellae. There are six pluripinnate branchial plumes. On the surface of the dorsal notum, Millen and Bertsch just mentioned some "rounded tubercles which are supported by spicules which protrude from the corners." Those tubercles may or may not caryophyllidia: The notum of specimens in collection is not well preserved and carytophyllidia can hardly be recognized. The radular formula of the paratype (CASIZ 074651) dissected by Millen and Bertsch is 23/24 × (42/63-0-42/63), for a 40 mm long, preserved specimen. More importantly, the rachidian space was properly described by Millen and Bertsch (2000: fig. 4C-D): "The central area has 12-15 small teeth per side, which abruptly increase in size and remain constant." The reproductive system does not present any peculiar feature, and more specimens will need to be dissected if we wish to find out how its general organization is diagnostic of *mullineri*. My re-examination of the reproductive system of the paratype CASIZ 074651 is similar to that of the paratype CASIZ 069302, illustrated by Millen and Bertsch. The prostate is divided in a distal part and a proximal part. The deferent duct is convoluted, with two distinct, distal loops. The bursa copulatrix is about three times as big as the receptaculum seminis. The latter, however, is smooth in the paratype CASIZ 074651 (instead of "distally nodular" in the paratype CASIZ 069302). The fertilization duct also is convoluted, with one loop near the bursa. Millen and Bertsch found and illustrated an "elongate common atrium" in the paratype CASIZ 069302, whereas the atrium of the paratype CASIZ 074651 is not strikingly elongated. Finally, Millen and Bertsch described a "thick, muscular, unarmed penis." The penial papilla likely just is the evaginable, distal part of the deferent duct instead of a permanent, distinct penis.

DIAGNOSTIC FEATURES.— The best diagnostic character of *mullineri* is the color of the dorsal notum, although we will certainly find in the future that this color does vary among individuals.

INFRA-SPECIFIC CHARACTER VARIATION.— Variation among individuals is unknown: the color of live animals was only observed in four individuals; the anatomy of *mullineri* is known from two specimens (if we count the present redescription of the reproductive system of the paratype CASIZ 074651); and the external morphology is only known from a few specimens.

DISCUSSION.— Although *mullineri* was described based on only four specimens, it seems to be distinct from other discodorids. However, more data are needed about the infra-specific character variation.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the position of *mullineri* shows that it belongs to the clade *Peltodoris*. Therefore, the Linnaean binomial should remain *Peltodoris mullineri*, which also is a possible name under the *ICPN*.

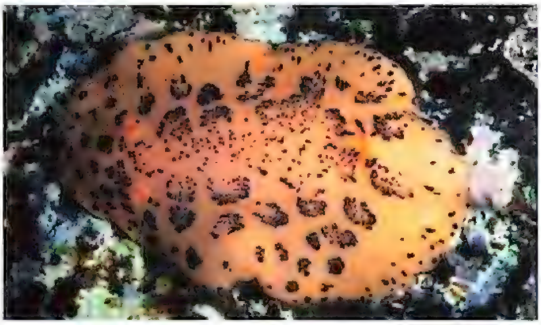

FIGURE 36. *Peltodoris mullineri*, dorsal color, holotype, CASIZ 074262 (T.M. Gosliner).

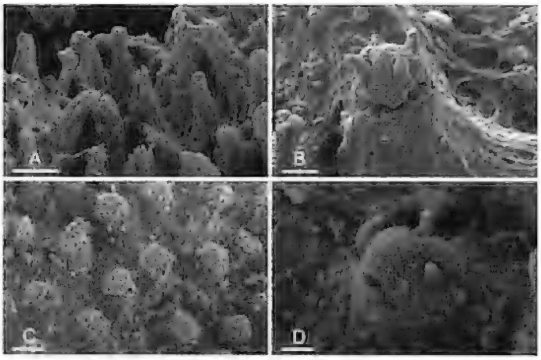

FIGURE 37. *Peltodoris mullineri*, dorsal notum. A. Paratype, CASIZ 074651, scale = 100 µm.— B. Paratype, CASIZ 074651, scale = 40 µm.— C. CASIZ 069302, scale = 100 µm.— D. Paratype, CASIZ 069302, scale = 20 µm.

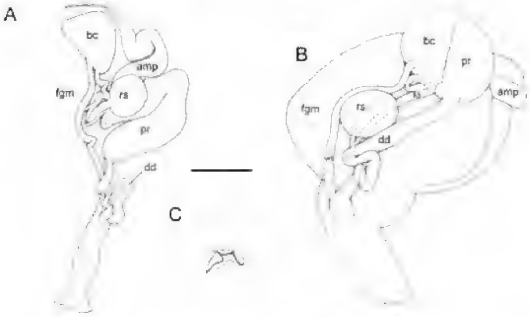

FIGURE 38. *Peltodoris mullineri*. A. Reproductive system, after Millen and Bertsch (2000: fig. 5), scale = 2.2 mm.— B. Reproductive system, paratype, CASIZ 074651, scale = 2 mm.— C. Anterior, ventral view, CASIZ 069302, scale = 12.5 mm.

***Peltodoris murrea* (Abraham, 1877) New combination**
Figures 39-52.

Doris murrea Abraham, 1877:252-253, plate XXVIII, figs 12-14.— Dorgan et al., 2002:41.
Platydoris ? *murrea*.— Bergh, 1878a:XXXI.
Peltodoris mauritiana Bergh, 1889:815-817.— Eliot, 1910a:420.— Edmunds, 1971:352-354, fig. 6. **New synonym.**
Discodoris mauritiana.— Orr, 1981:46, unnumbered figure.
Discodoris ? *mauritiana*.— Yonow, 2008:274, two unnumbered figures.
Discodoris cf. *mauritiana*.— Marshall and Willan, 1999:73-74, fig. 124.— Yonow and Hayward, 1991:17-18, figs 7C, 8A-C.
Discodorididae mauritiana.— Dayrat and Gosliner, 2005:205.
Discodoris fragilis.— Willan and Coleman, 1984:36, fig. 112 [not *fragilis* Alder and Hancock, 1864].

TYPE MATERIAL (*murrea*).— Two syntypes: one specimen 37/22 mm preserved, leg. Mr. Cutter, [no collecting date], [this specimen was formerly labeled as the holotype], (NHM 1876.2.5.2); one specimen 35/20 mm preserved, leg. Mr. Cutter, [no collecting date], [this specimen was labeled as the paratype], (NHM 1876.2.5.3). As pointed out by Dorgan et al. (2002), the type specimens of *murrea* are syntypes because Abraham did not designate a holotype.

TYPE MATERIAL (*mauritiana*).— Six syntypes: from 20/15 to 45/25 mm preserved, [no leg.], [no collecting date], (ZMB 43931).

TYPE LOCALITY (*murrea*).— Mauritius, [Indian Ocean].

TYPE LOCALITY (*mauritiana*).— Mauritius, [Indian Ocean].

TYPE MATERIAL CONDITION (*murrea*).— Contrary to what Dorgan and co-authors (2002) asserted, the type specimens of *murrea* are well preserved. Abraham dissected one syntype (the former "holotype") of *murrea*, and left all the internal organs in the jar, except for the radula which is probably lost (no slide was found at the NHM). The reproductive system of the specimen dissected by Abraham was drawn for the present study. The other syntype (the former "paratype"), entire and in good external condition, was not dissected for the present study.

TYPE MATERIAL CONDITION (*mauritiana*).— All specimens were dissected prior to the present study and are now empty body walls.

ADDITIONAL MATERIAL DISSECTED.— **Madagascar**, Mora Mora, Barrier Reef, 20 March 1990, one specimen 19/7 mm preserved [part of the notum, removed, is missing], leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 073317); **Indian Ocean**, Mascarene Islands, Reunion Island, Saint-Gilles les Bains, 20 April 1989, one specimen 60/32 mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 070389); Indian Ocean, Cocos Islands (Keeling), West Island, 12°10′S, 96°49′E, 29 March 1982, two specimens 30/24 (#1) and 14/10 (#2) mm preserved, leg. J. Hicks, identified as *Discodoris* by W. B. Rudman (AM C133485); **Thailand**, Andaman Sea, southern end of Phuket Island, Rawaii Beach, 22 March 1985, one specimen 26/22 mm preserved, leg. Kit Stewart, identified as *Discodoris* by T. M. Gosliner (CASIZ 073508) [reproductive system poorly preserved]; **Australia**, Queensland, Grand Barrier Reef, south end of Day Reef, 14°31′S, 145°32′E, 15 meters depth, 12 December 1984, one specimen 25/17 mm preserved, leg. I. Loch, identified as *Discodoris* cf. *concinna* by W. B. Rudman (AM C144547) [reproductive system poorly preserved]; Australia, Queensland, Bingil Bay, south end of beach, East of El Arish, 17°50′S, 146°6′E, 15 meters depth, 2 June 1977, one specimen 25/17 mm preserved, leg. I. Loch, identified as *Discodoris* by W. B. Rudman (AM C107821); Australia, Queensland, Heron Island, south side, 23°27 ′S, 151°55′E, 3 December 1996, one specimen 30/22 preserved [40 mm alive], leg. Julie Marshall, identified as *Discodoris* cf. *mauritiana* by Julie Marshall (NMV F80593) [this specimen is a voucher designated by Marshall and Willan (1999)]; **New Caledonia**, Baie de Touho, 20°46.5′S, 165°14′E, 1-4 meters depth, September 1993, Stn 1252, two specimens 38/22 (#1) and 32/18 (#2) mm preserved, leg. Expedition Montrouzier, not identified [an unknown identifier wrote the name '*Discodoris fragilis*' on a piece of paper that also indicates the existence of "*4 ex*," i.e., probably for 4 specimens, although only two specimens were available] (MNHN, no catalogue number); **Japan**, Ryukyu Islands, Okinawa, 1.3 km ENE of Maekizaki, Seragaki Beach, 26 May 1991, one specimen 37/17 mm preserved length, leg. R. F. Bolland, identified as *Discodoris* by T. M. Gosliner (CASIZ 079243); Japan, Ryukyu Islands, Okinawa, 1.3 km ENE of Maekizaki, Seragaki Beach, 26 May 1991, one specimen 26/17 mm preserved length, leg. R. F. Bolland, identified as *Discodoris* by T. M. Gosliner (CASIZ 079249).

DISTRIBUTION.— Tropical Indo-West Pacific. Red Sea (Yonow, 2008, as *mauritiana*), Tanzania (Edmunds 1971, as *mauritiana*), Madagascar (present study), Reunion (present study), Mauritius (Abraham 1877; Bergh 1889, as *mauritiana*; Yonow and Hayward 1991, as *mauritiana*), Chagos Archipelago (Eliot 1910a, as *mauritiana*), Cocos (Keeling) Islands (present study), Queensland (Willan and Coleman 1984, as *fragilis*; Marshall and Willan 1999, as *mauritiana*; present study), Hong Kong (Orr 1981, as *mauritiana*), Thailand and New Caledonia (present study). Also, its presence in warm waters of Japan, suggested by Baba (1937a, 1937b, as *mauritiana*), is confirmed here. Marshall and Willan (1984) thought that Bertsch and Johnson (1981:40) had misidentified specimens of *mauritiana* as *fragilis*. These specimens have been misidentified, but their real name is *lilacina* (see this species). Six specimens from Singapore and Malaysia, identified as *Discodoris palma* by Lim and Chou (1970), may be part of *murrea*, although it is uncertain: the drawing of the dorsal notum provided by the authors is compatible with *murrea*. Finally, note that the specimen identified as *Discodoris* cf. *mauritiana* by Coleman (2001) is part of *coerulescens*.

WWW.— A specimen identified as *Discodoris* cf. *mauritiana* on the website of the Opisthobranchs of the Kii Peninsula clearly is part of *coerulescens*.

OCCURENCE.— The species *murrea* is relatively well represented in museum collections (see above) and has been regularly mentioned in the literature. However, the fact that no picture has been posted on the *www* seems to indicate that it is not a common species. Marshall and Willan (1999, as *mauritiana*) mention that it is rare in Heron Island, Queensland. It seems that *murrea* is not common, but widespread.

HABITAT.— Most specimens dissected here were collected in the intertidal zone, although one specimen was found at 15 meters depth. Marshall and Willan (1999, as *mauritiana*) mentioned that *murrea* is commonest at low intertidal level, but could be found up to 21 meters. Some specimens were found under small rocks (NMV F80993), under stone on silty rocky shore (AM C107821). Marshall and Willan (1999) found *murrea* on "coral substrates… under dead coral slabs, either at reef crest or beach rock."

LITERATURE.— Several authors have provided some information about the color of the dorsal notum (Abraham 1877; Bergh 1889, as *mauritiana*; Eliot 1910a, as *mauritiana*; Edmunds 1971, as *mauritiana*; Orr 1981, as *mauritiana*; Willan and Coleman 1984, as *mauritiana*; Marshall and Willan 1999, as *mauritiana*); the last three contributions include color pictures. However, the diagnostic character of *murrea* was never pointed out, which probably explains misidentifications (e.g., Willan and Coleman 1984) and uncertainties (e.g., Marshall and Willan 1999). Abraham (1877) and Eliot (1910a) provided brief information about the radula; Bergh (1889) and Edmunds (1971) provided some anatomical data. Baba (1937a, 1937b) recorded *Peltodoris mauritiana* in warm Japanese waters, but did not provide any description that could help us verify that he saw specimens of *murrea*. Narayanan (1971) mentions *Peltodoris mauritiana* in a paper where *Peltodoris rubescens* Bergh is described. Jensen (1998) also cites *mauritiana* in a paper on the biogeography of Hong Kong.

REMARKS ON THE ORIGINAL DESCRIPTION (*murrea*).— Contrary to Dorgan and co-authors' (2002) statement, the original description of *murrea* by Abraham provides valuable information. In particular, one of Abraham's black-and-white drawings (Figs. 39D-E) properly illustrates what he described as an "ample, cartilaginous" white notum with an "opaque greyish marbling." As a matter of fact, there is a clear similarity between Abraham's drawing and some pictures of living animals (e.g., Orr 1981, as *mauritiana*). This marble-like pattern on the dorsal notum, still distinguishable on the type specimens, is diagnostic of *murrea*. The small brown dots may have disappeared with preservation (see below the description of new specimens). Abraham provided several general features, such as the presence of hard, rounded tubercles on the dorsal surface, six bipinnate gills, a completely contractile gill pocket, small, conical, and pointed oral tentacles, and an anterior foot bilabiate with a notched upper lip. The number of rhinophoral lamellae could not be determined. Abraham also described and represented radular teeth with bases "laterally flattened," which can be interpreted as the spur on the base of the innermost lateral teeth (see below). Abraham did not describe the reproductive system: its organization is similar to that of the additional specimens dissected for the present study; in particular, the convoluted deferent duct is in the exact same position (Fig. 49).

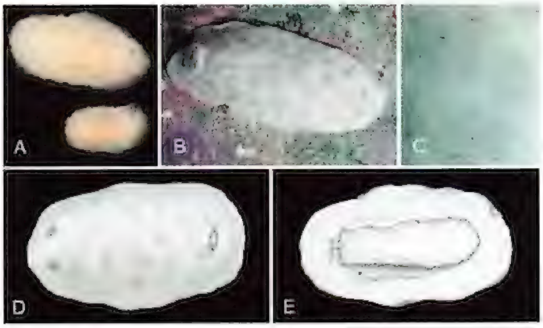

FIGURE 39. *Peltodoris murrea*, dorsal views (except E). A. CASIZ 079243 (top), total length = 37 mm long (alive), and CASIZ 079249, total length = 26 mm long (alive).— B. CASIZ 070389, total length = 60 mm (preserved).— C. Detail, CASIZ 070389.— D. Dorsal view of one of the syntypes, Abraham (1877: plate XXVIII, fig. 12).— E. Ventral view of one of the syntypes, Abraham (1877: plate XXVIII, fig. 13).

REMARKS ON THE ORIGINAL DESCRIPTION (*mauritiana*).— Bergh's description certainly is not brief, but the absence of figures makes it difficult to use. However, the combination of two characters is informative: the color of the dorsal notum ("yellowish with transparent, ashen large spots"), which Bergh rightly considered as diagnostic, and the radular teeth that Bergh rightly described as similar to that of *atromaculata*. Now, the color of preserved animals is homogeneously white, unfortunately. The radular formula provided by Bergh was 23/26 × (34/40-0-34/40). In the reproductive system, Bergh mentioned the presence of a "conical, unarmed penis."

DESCRIPTION OF NEW SPECIMENS (Figs. 39-52).— *Color*. The ground color of the dorsal notum is creamish bearing pale gray marble-like blotches and a few small dark brown dots. After preservation, the brown dots may disappear (e.g., AM C133485, CASIZ 070389) or remain (e.g., MNHN, CASIZ 079243). However, the marble-like pattern of the ground color, with a distinction between the creamish ground color and the pale grey blotches, is always recognizable after preservation. Preserved, the hyponotum and the foot are creamish, although they also may also bear brown dots.

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform but not grooved. The dorsal notum bears tubercles that are not caryophyllidia, but those tubercles are embedded in a thick, cartilaginous-like matrix. As a result, the notum may seem to be smooth. Tubercles are easier to observe on the edges of the notum. Many small holes (diameter < 10 μm) and many small tufts of cilia are present on the surface of the mantle, including the tubercles, the gills, and the rhinophores. In preserved specimens, the margins of the rhinophoral sheaths can be smooth or lightly crenulate. There are six bi- or tripinnate branchial plumes arranged in circle around the anus. However, the exact number of gills could hardly be established in several specimens because the gills were deeply retracted. The rhinophores have up to 20 lamellae.

Digestive system. In several specimens, the oral tube was at least three or four times longer

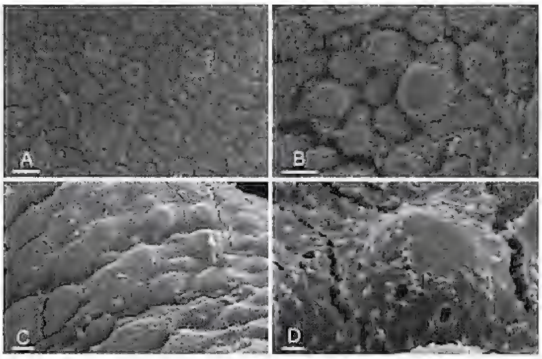

FIGURE 40. *Peltodoris murrea*, dorsal notum, tubercles. A. MNHN (#1), scale = 200 µm.— B. MNHN (#1), scale = 100 µm.— C. MNHN (#1), scale = 100 µm.— D. CASIZ 070389, scale = 20 µm.

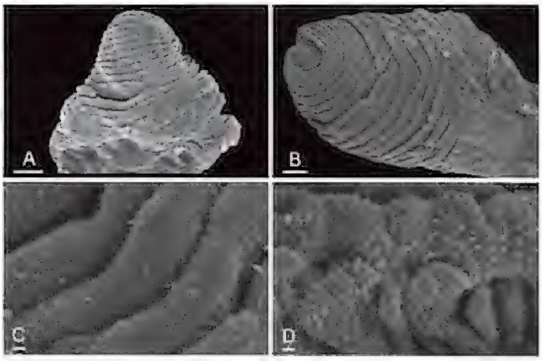

FIGURE 41. *Peltodoris murrea*, rhinophores and gills. A. Rhinophore, CASIZ 073508, scale = 200 µm.— B. Rhinophore, CASIZ 070389, scale = 200 µm.— C. Rhinophoral lamellae, CASIZ 070389, scale = 10 µm.— D. Branchial plume, detail, CASIZ 070389, scale = 20 µm.

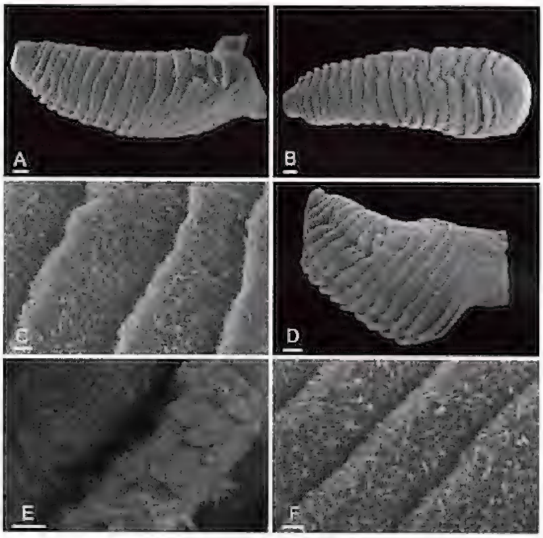

FIGURE 42. *Peltodoris murrea*, rhinophores. A. MNHN (#1), scale = 100µm.— B. MNHN (#1), scale = 100 µm.— C. Rhinophoral lamellae, MNHN (#1), scale = 20 µm.— D. MNHN (#2), scale = 100 µm.— E. Rhinophoral lamellae, MNHN (#2), scale = 10 µm.— F. Rhinophoral lamellae, MNHN (#2), scale = 20 µm.

than what was found in all other species examined (e.g., CASIZZ 073317, AM C107821). This could be a natural feature related to the feeding habits of *murrea*. The stomach is free, on top of the digestive gland, on the left. A small caecum is located on the left-posterior side of the stomach. The intestine is straight and dorsal. The digestive gland was dark bright orange in all specimens but three (NMV F80593, MNHN). Given that all these specimens were fixed and preserved in different ways, this unusual color is probably natural and due to feeding habits. The labial cuticle is smooth. The color of the labial cuticle is confusing though. It was white (e.g., MNHN), as in most smooth labial cuticles, or brown (e.g., CASIZ 073317, AM C144547, AM C107821). The radula is square-shaped: its length is a little bit longer than its width. The radular sac cannot be seen by dorsal dissection. Radular formulae are: e.g., 14 × (31-0-31) in a 14 mm long specimen (AM C133485 #2), 15 × (28-0-28) in a 32 mm long specimen (MNHN #2), 17 × (32-0-32) in a 25 mm long specimen (AM C107821), 18 × (31-0-31) in a 26 mm long specimen (CASIZ 073508), 18 × (33-0-33) in a 37 mm long specimen (CASIZ 079243), 18 × (34-0-34) in a 19 mm long specimen (CASIZ 073317), 18 × (40-0-40) in a 30 mm long specimen (AM C133485 #1), 19 × (30-0-30) in a 38 mm long specimen (MNHN #1), 19 × (35-0-35) in a 30 mm long specimen (NMV F80593), 20 × (35-0-35) in a 25 mm long specimen (AM C144547), 23 × (32-0-32) in a 60 mm long specimen (CASIZ 070389). Rachidian teeth are absent. The rachidian space is narrow. However, there is a wide space in which the innermost teeth are reduced in size, creating a sort of pseudo-rachidian space. The lateral teeth are at an angle of 90 degrees with the rachidian axis, except for all the reduced innermost teeth, which can be at an angle of less than 45 degrees.

The size of the first ten innermost teeth is quite reduced compared to the median teeth. In some cases, the difference in size between the innermost lateral teeth and the median teeth is obvious (e.g., CASIZ 079243), and in other cases it is slightly attenuated (e.g., MNHN #1). Then the size of the teeth suddenly increases (approximately, from the ninth to the fifteenth tooth), stays approximately constant, and finally decreases for the last three or five innermost teeth. The last two outermost teeth may be vestigial. The teeth bear no denticles, nor are they grooved. However, the base of the reduced innermost teeth bears a distinct spur.

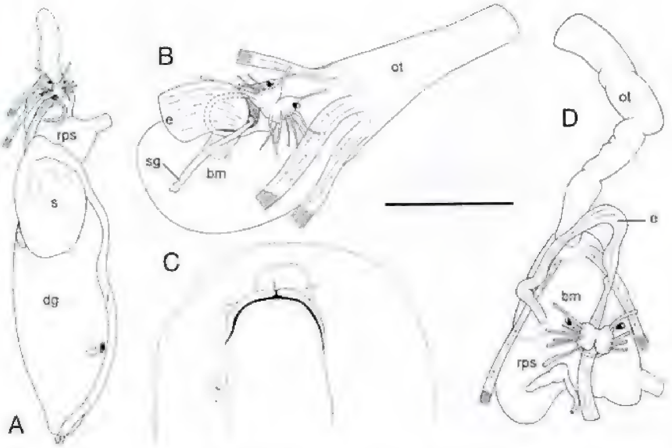

FIGURE 43. *Peltodoris murrea*. A. General anatomy, CASIZ 070389, scale = 1.6 mm.— B. Buccal mass and nervous system, CASIZ 073317, scale = 3.5 mm.— C. Ventral, anterior view, CASIZ 070389, total width = 30 mm.— D. Buccal mass, reproductive system, and nervous system, CASIZ 073317, scale = 4 mm.

Nervous system. The length of the circum-esophageal nerve ring equals from one up to three times the width of the two cerebro-pleural ganglia. The cerebral and pleural ganglia are fused; they may or may not be separated from the pedal ganglia. Their surface is smooth.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. Fully mature reproductive systems look like a gigantic whitish female gland mass bearing on its side the other inconspicuous structures (bursa copulatrix, receptaculum seminis, prostate, ducts). Consequently, several features were difficult to observe in fully developed reproductive systems, which was almost impossible when they were poorly preserved (e.g., C144547, CASIZ 073508, NMV F80593). However, all connections were easy to observe in smaller specimens with a small female gland mass (e.g., MNHN #2, C133485 #2). The ampulla is short or loosely convoluted. The division between male and female ducts, embedded within the female gland mass, could not be seen by dissection. The prostate is divided in a proximal whitish part and a distal yellowish part. The deferent duct of fully mature individuals is straight in its first part, and then loosely convoluted with a few (about five) loops near the penial sheath. It also is narrow and fragile. The organization of the deferent duct is easily recognizable and present in all fully mature specimens. However, the deferent duct seems to be

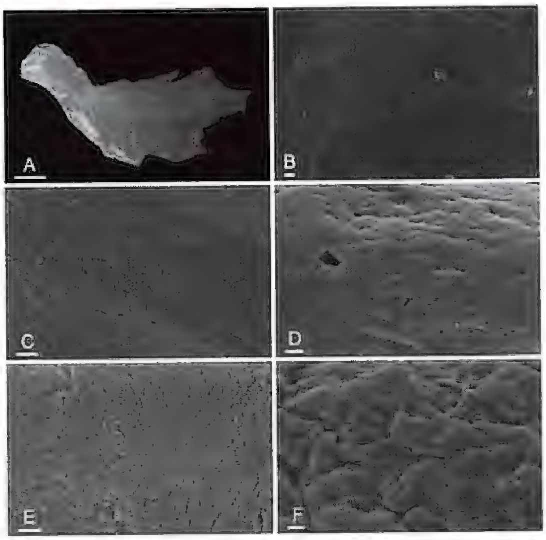

FIGURE 44. *Peltodoris murrea*, smooth labial cuticle. A. CASIZ 070389, scale = 1 mm.— B. AM C107821, scale = 20 µm.— C. CASIZ 073508, scale = 20 µm.— D. MNHN (#1), scale = 10 µm.— E. AM C133485 (#1), scale = 10 µm.— F. CASIZ 073317, scale = 10 µm.

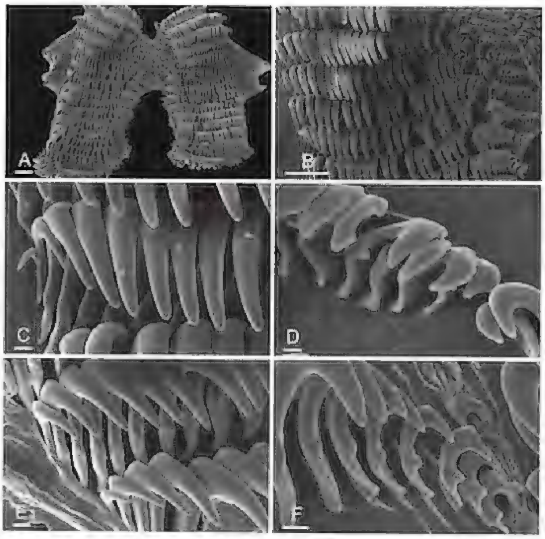

FIGURE 45. *Peltodoris murrea*, radula. A. CASIZ 073508, scale = 200 µm.— B. Left rows, CASIZ 073508, scale = 200 µm.— C. Outermost teeth, CASIZ 073508, scale = 20 µm.— D. Innermost teeth, CASIZ 073508, scale = 10 µm.— E. Outermost teeth, CASIZ 079243, scale = 30 µm.— F. Innermost teeth, CASIZ 079243, scale = 20 µm.

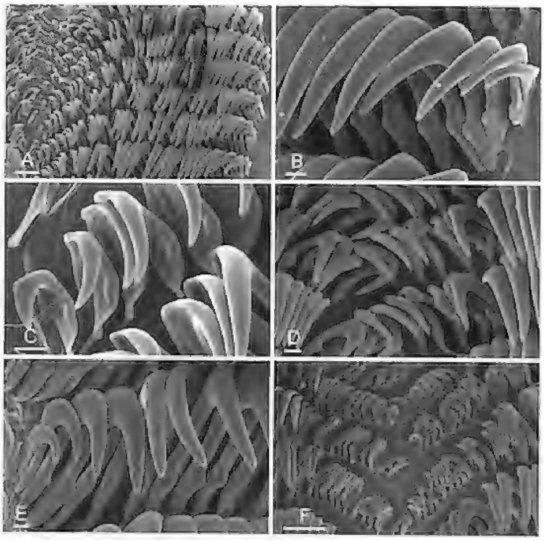

FIGURE 46. *Peltodoris murrea*, radula. A. Right rows, MNHN (#1), scale = 100 µm.— B. Outermost teeth, MNHN (#1), scale = 20 µm.— C. Innermost teeth, MNHN (#1), scale = 20 µm.— D. Innermost teeth, MNHN (#2), scale = 10 µm.— E. Outermost teeth, CASIZ 073317, scale = 20 µm.— F. Innermost teeth, CASIZ 073317, scale = 100 µm.

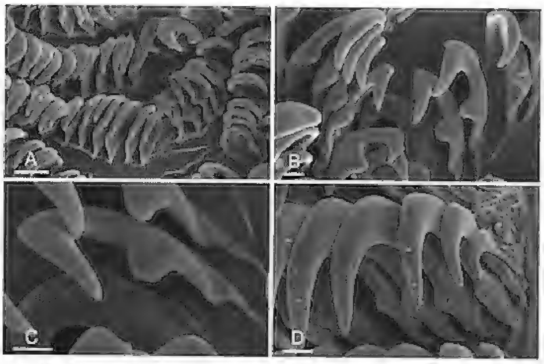

FIGURE 47. *Peltodoris murrea*, radula. A. Innermost teeth, AM C144547, scale = 30 µm.— B. Innermost teeth, AM C144547, scale = 10 µm.— C. Innermost teeth, AM C144547, scale = 10 µm.— D. Outermost teeth, AM C144547, scale = 30 µm.

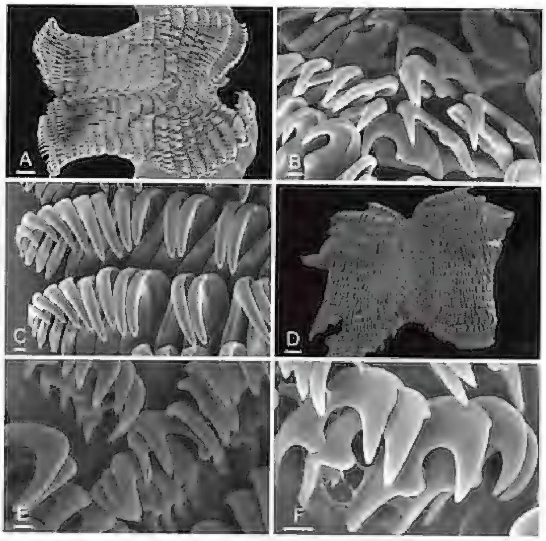

FIGURE 48. *Peltodoris murrea*, radula. A. MV F80593, scale = 200 µm.— B. Innermost teeth, MV F80593, scale = 10 µm.— C. Outermost teeth, MV F80593, scale = 20 µm.— D. AM C133485 (#1), scale = 200 µm.— E. Innermost teeth, AM C133485 (#2), scale = 10 µm.— F. Innermost teeth, AM C107821, scale = 10 µm.

longer and is more tightly convoluted in not fully mature specimens (MNHN #2, AM C133485 #2). This difference between not fully mature and fully mature specimens could be explained by the fact that the deferent duct could stop growing when the female gland mass starts expanding. The shape of penis varies a great deal: conical, with no humps on its surface, ciliated on its first half, and 0.85 m long (CASIZ 070389); conical, with no humps on its surface, completely ciliated, and 0.36 mm long (NMV F80593); a large conical base and a long, slender apex, 0.6 mm in total length (CASIZ 079243); a strong, ovate base and a narrow apex, 0.54

mm in total length (CASIZ 073317); conical, with a wide, flat tip (instead of pointed) and a large crown of at mid length (probably caused by the retraction of the penis), 0.14 mm in total length (AM C107821); elongate (MNHN); elongate, completely covered with cilia, and with a few, small, distal humps (CASIZ 074249); with a strong, ovate, ciliated base, and a smooth conical apex (delimited by a crown of small humps), 0.4 m in total length (AM C133485 #1); conical, ciliated base with a smooth cap (ciliated at the apex) that looks delimited by a crown of humps (AM C133485 #2). Note that no penial organ could be found in one specimen (AM C144547) and the penis of the specimen from Thailand could be observed because the distal part of its reproductive system was not well preserved. The vaginal duct is straight, although it is loosely convoluted in the specimens with a smaller female gland masss (MNHN #2, AM C133485 #2). The fertilization duct is straight and short, although it is coiled near the bursa copulatrix in two specimens with a small female gland mass (MNHN #2, AM C133485 #2). The connection between the fertilization duct and the female gland mass is marked by a short duct. Both the connection of the receptaculum seminis duct to the receptaculum seminis and the disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) are underneath the receptaculum seminis. The size of the bursa copulatrix equals up to three times the size of the receptaculum seminis, but usually is just slightly larger. In occasion, the receptaculum seminis may also be slightly larger than the bursa (MNHN #2). Both spermatic pouches are spherical-ovate, close to each other, but not necessarily attached.

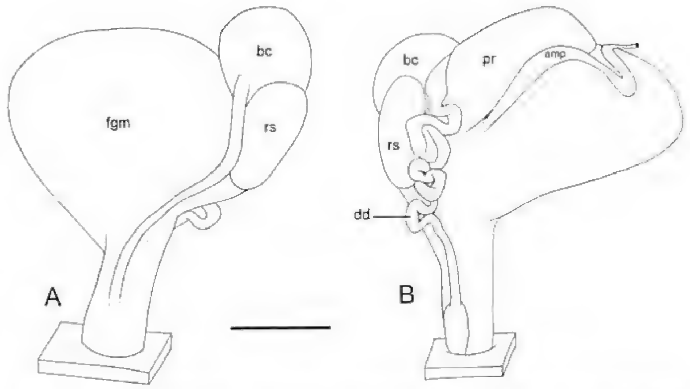

FIGURE 49. *Peltodoris murrea*, reproductive system, syntype, NHM 1876.2.5.2. A. Scale = 2 mm.— B. Scale = 2 mm.

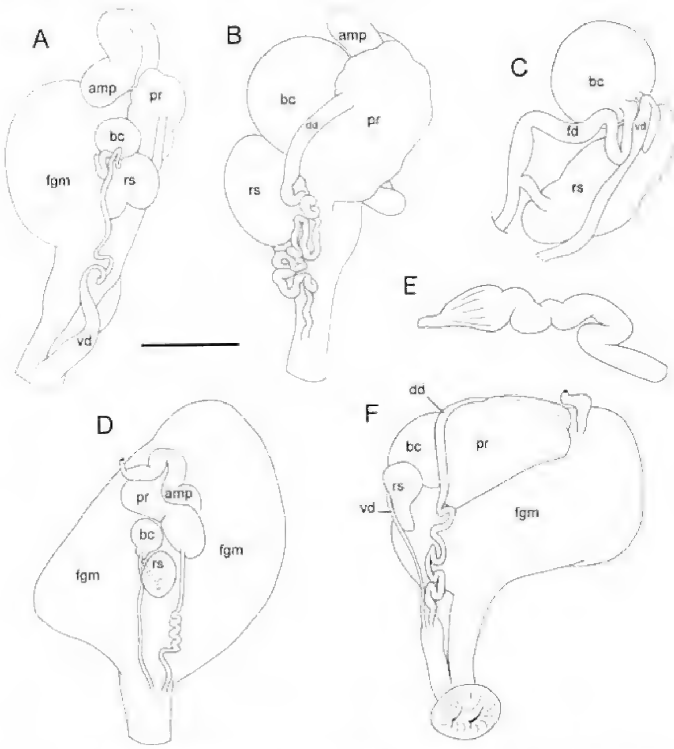

FIGURE 50. *Peltodoris murrea*, reproductive system. A. CASIZ 079249, scale = 1.5 mm.— B. AM C133485 (#2), scale = 0.8 mm.— C. Spermatic pouches and ducts, CASIZ 079249, scale = 0.5 mm.— D. MNHN (Touho), scale = 1 mm.— E. CASIZ 070389, scale = 4 mm.— F. Distal deferent duct and papilla, scale = 1.3 mm.

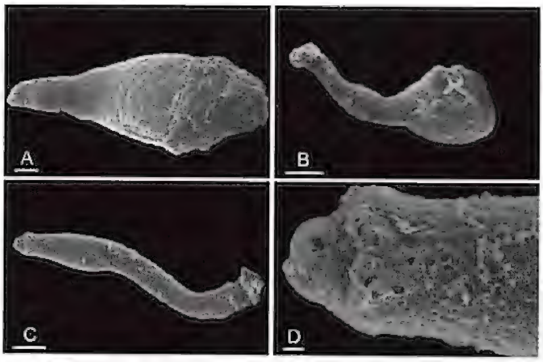

FIGURE 51. *Peltodoris murrea*, penis. A. CASIZ 070389, scale = 100 µm.— B. CASIZ 079243, scale = 100 µm.— C. CASIZ 079249, scale = 100 µm.— D. CASIZ 079249, scale = 10 µm.

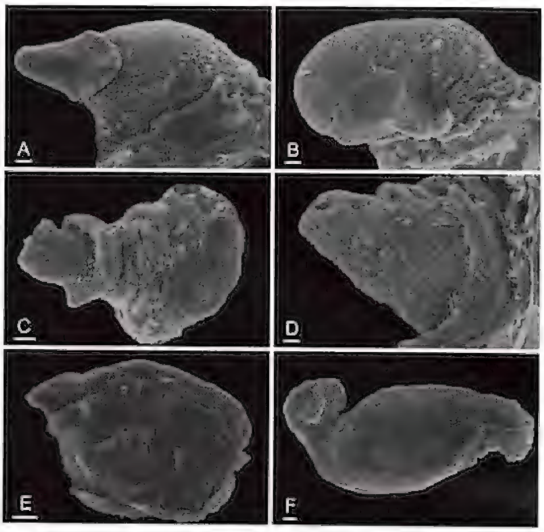

FIGURE 52. *Peltodoris murrea*, penis. A. AM C133485 (#2), scale = 20 µm.— B. AM C133485 (#1), scale = 20 µm.— C. AM C107821, scale = 20 µm.— D. MV F80593, scale = 20 µm.— E. MNHN (#2), scale = 20 µm.— F. CASIZ 073317, scale = 30 µm.

DIAGNOSTIC FEATURES.— The color of the dorsal notum (from whitish to light-tan ground color with marble-like pale grayish blotches and a few small brown dots) is typical of *murrea*. It can hardly be confused when pictures of living animals are available or when specimens are well preserved. However, poorly preserved specimens of *murrea* may be confused with *Discodorididae coerulescens*. A potentially good external character to separate preserved specimens of *coerulescens* and *murrea* is that the dark spots found on the dorsal surface of *coerulescens* are smaller than the marble-like blotches of *murrea*; another difference is that the notum of *coerulescens* is covered with tubercles, whereas the tubercles of the notum of *murrea* are embedded within a sort of cartilaginous matrix. In any case, these two species have a different anatomy, and should no longer be confused in the future. Internal diagnostic characters of *murrea* are: the organization of the loosely convoluted deferent duct (in fully mature specimens only), and the dark, bright, orange digestive gland (not in all preserved specimens though). The small, innermost lateral teeth bearing a spur are not diagnostic of *murrea* in the strict sense because they also are found in some other species, such as *Peltodoris atromaculata*.

INFRA-SPECIFIC CHARACTER VARIATION.— Anatomical and morphological data available in the literature are compatible with the present description. The radular formulae provided in the literature were: 23/26 × (34/40-0-34/40) in individuals from 20 to 43 mm long (original description of *mauritiana*; Bergh 1889), 21 × (35-0-35) and 28 × (40-0-40) in 40 mm long specimens (Eliot 1910a), and 19 × (31-0-31) in a 27 mm long specimen (Edmunds 1971). Overall, the number of rows varies from 14 (present study) to 26 (Bergh's original description of *mauritiana*), and the number of teeth per row varies from 28 (present study) to 40 (Bergh 1889; present study). The illustration of the reproductive system published by Edmunds (1971) can hardly be used for comparison because it is too schematic. Moreover, Edmunds (1971) stated that the reproductive system of *mauritiana* (i.e., *murrea*) was close to that of *Discodorididae coerulescens*. In *coerulescens*, the hermaphroditic gland is independent from the digestive gland and attached to the rest of the reproductive system, which is a major difference with *murrea*. Edmunds did not misidentify specimens. However, he could not evaluate differences and similarities because he only dissected one or two specimens. Finally, the shape of the penis of *murrea* is highly variable. Based on the available data, there is no reason to think that the reason to think that it is anything else than infra-specific variation. However, phylogeographic data could unveil several, closely related, cryptic *murrea*-like species.

Discussion.— The drawing published by Abraham for *murrea* and the re-examination of the type material made the identification of the non-type specimens easier. Traditionally, the specimens with such a dorsal color have been identified as *mauritiana*. The synonymy of both species names is supported not only by this tradition but also by Bergh's precise description of the color. Interestingly, the fact that Bergh (1878a) arbitrarily (i.e., without looking at the type material) placed *murrea* within *Platydoris* prevented him from realizing that his new species *mauritiana* was just a synonym of *murrea*. The identification of a specimen of *Discodoris* cf. *mauritiana* by Yonow and Hayward (1991) is accepted here, although it is uncertain: they did not describe the typical marble-like dorsal pattern, but the presence of small black dots on grey areas could be regarded as an identification of *murrea*. In any case, it does not really matter because we already know that *murrea* is present in Mauritius. Yonow (2008) recently published a picture of "*Discodoris* ? *mauritiana*" from the Red Sea which clearly is part of *murrea*.

Supra-specific relationships.— Bergh (1878a) decided to re-allocate *murrea* from *Doris* to *Platydoris* but did not explain his reasons. Dorgan and co-authors (2002) argued that *murrea* did not belong to *Platydoris*: indeed, none of the diagnostic characteristics of *Platydoris* is found in *murrea*. A phylogenetic test of the position of *murrea* shows that it belongs to the clade *Peltodoris*. Therefore, the Linnaean binomial should remain *Peltodoris murrea*, which also is a possible name under the *ICPN*.

Tayuva Marcus and Marcus, 1967

Under the *ICZN*, *Tayuva* is a taxon of genus-level. Type-species: *Tayuva ketos* Marcus and Marcus, 1967, by original designation.

The phylogenetic diagnosis of *Tayuva* includes four classes of characters, depending on their phylogenetic significance. 1) One synapomorphy exclusively found in this taxon: a muscular wall in the distal portion of the reproductive system; only this synapomoropohy can be regarded as diagnostic of *Tayuva* (i.e., only this character can be used to identify that a species belongs to *Tayuva*). 2) One synapomorphy found in *Tayuva*, but also found in other species: a wide, proximal part of the deferent duct, folded internally (also found in some specimens of *Sebadoris nubilosa* and possibly in *Discodorididae muta* and *Discodorididae golaia*). 3) Four synapomorphies of *Discodorididae*: a notched upper lip of the bilabiate anterior foot, digitiform or conical oral tentacles that are *not* expansions of the lateral mouth lips, a flattened prostate divided in two parts of distinct color, and two blood glands. 4) Characters found in many other dorid nudibranchs, e.g., absence of rachidian teeth, hamate lateral teeth, etc. Finally, the prostate of *Tayuva* is most often divided in three parts (instead of two in other discodorids), but this division in three parts is not consistently found in all specimens, so it cannot be regarded as diagnostic *per se* (an individual with a prostate divided in two parts can belong to *Tayuva*).

In the present contribution, *Tayuva* as a (monotypic) clade name, without being assigned to any particular rank. Under the *ICPN*, *Tayuva* is a converted clade name: it remains an informal clade name until it is phylogenetically defined *and* formally registered. *Tayuva* could be phylogenetically defined through an apomorphy-based definition as "the clade stemming from the first organism or species to possess a muscular wall in the distal region of the reproductive system as inherited by *Tayuva ketos* Marcus and Marcus, 1967." Note that *ketos* currently is a synonym of *lilacina*, but it is used as the specifier here in congruence with the *ICZN* type species.

The taxonomy of *Tayuva* is quite special. Animals belonging to *Tayuva* are found almost worldwide (Mediterranean, eastern and western Atlantic, tropical eastern Pacific, and tropical

Indo-West Pacific). However, no species can be distinguished among all specimens based on anatomy or external morphology: e.g., without knowing their geographical distribution, animals from Panama will certainly be confused with animals from the Mediterranean. Morphology alone does not help determine the number of species that belong to *Tayuva*. There could be from a single widely-distributed species up to many species, including cryptic ones. At present, eight specific names and three subspecific names are available within *Tayuva*. Misidentifications are common in the literature: animals were identified with a *Tayuva* specific name, such as *lilacina*, although they do not belong to *Tayuva*; reciprocally, animals were identified with a non-*Tayuva* specific name, such as *fragilis*, although they do belong to *Tayuva*.

Only one widely-distributed species is accepted here, *Tayuva lilacina* (Gould, 1852), mainly because of the absence of anatomical features available to distinguish species. At this stage, all other specific and subspecific names referring to taxa that belong to *Tayuva* should be regarded as synonyms.

It is very likely that there are more than one species in *Tayuva*, especially in the Indo-West Pacific where some subtle variations among specimens indicate that cryptic species might exist. The name *Tayuva lilacina*, as used here, likely refers to a species complex. However, other tools will be needed to sort out the *Tayuva* species diversity. A phylogeographic study of this group, based on markers traditionally used at this level (e.g., CO1), is critically needed.

The presentation of *Tayuva lilacina* is split here in four sections, based on geographic distribution: Caribbean Sea, eastern Pacific, tropical Indo-West Pacific, and Mediterranean and European eastern Atlantic. The main reason for this organization is that each of these regions presents specific issues which are more easily discussed at a regional context than in a global context. Also, most readers will be interested in the fauna of a particular region, and will thus have directly access to the nomenclature, specimens, and issues related to each region.

***Tayuva lilacina* (Gould, 1852)**
Region: Caribbean Sea
Figures 53A, 54-61.

Peltodoris crucis.— Bergh, 1880a:41-46, plate A, figs 1-2 [in part, not *crucis* Ørsted *in* Mörch, 1863:33].
Peltodoris hummelincki Marcus and Marcus, 1963:27-30, 67, figs. 32-35. **New synonym.**
Tayuva ketos gila Marcus and Marcus, 1970a:2, 65-66, figs 118-120. **New synonym.**

TYPE MATERIAL (*hummelincki*).— The type material of *hummelincki* includes a holotype, by original designation, and four paratypes. Eveline and Ernst Marcus deposited three type specimens at the Zoölogisch Museum, Amsterdam, one holotype and two paratypes, all from the same locality (Santa Marta Baai, Curaçao). The body wall of a third paratype (dissected by Eveline and Ernst Marcus) from the same locality was kept at the University of São Paulo, but the radula was sent to the Zoölogisch Museum, Amsterdam, which no longer holds it. A fourth paratype from another locality (Piscadera Baai, Curaçao) and dissected by Eveline and Ernst Marcus was kept in São Paulo too. The body wall of the third paratype as well as the fourth paratype should be in the collection of the Museu de Zoologia da Universidade de São Paulo. No type material of *hummelincki* could be found at this institution. However, it does not mean that it is lost because the nudibranch collection has not been completely curated (personal communication, Dr. Luiz Simone). Holotype (ZMA Moll. 3.63.020), by original designation: one specimen 42/28 mm preserved, leg. Pieter Wagenaar Hummelinck, 3 March 1955. Two paratypes (ZMA Moll. 3.63.021): two specimens 45/35 (#1) and 25/20 (#2) mm preserved, leg. Pieter Wagenaar Hummelinck, 3 March 1955. Note that the Marcus mentioned four additional non-type specimens in the original description.

Type material (*ketos gila*).— The original description mentions two syntypes (26 and 15 mm long, preserved) collected in Curaçao (leg. not indicated) on 22 December 1965 and 26 January 1966. The MZSP holds two specimens that most likely are those two syntypes, although they were not labeled as syntypes: they are from the Marcus' collection (#419/C19); they were collected in 1966 from Curaçao. Two syntypes (MZSP 43478): two specimens 22/13 (#1) and 16/6 (#2) mm, leg. Diva Corrêa, 1966.

Type locality (*hummelincki*).— Santa Marta Baai, Curaçao, Caribbean Sea. Three paratypes also come from this locality (two paratypes preserved at the ZMA [ZMA Moll. 3.63.021], and possibly a third paratype held by the MZUSP). A fourth paratype, possibly held by the MZUSP, was collected from Curaçao too, but from another locality, Piscadera Baai. Two additional non-type specimens, mentioned in the original description, were collected from Curaçao: one from Santa Marta Baai, one from Rifwater. Finally, two other non-type specimens, mentioned in the original description, were collected from Aruba.

Type locality (*ketos gila*).— Piscadera Baai, outer bay, Curaçao, Caribbean Sea (based on the original description). The label of the two MZSP specimens identified here as the two syntypes simply indicates: "Curaçao, Caribe."

Type material condition (*hummelincki*).— The three type specimens held by the ZMA are entire and well preserved externally. The holotype was opened laterally here to verify that its reproductive system had the diagnostic features of *Tayuva* and that this specimen did not belong to another species (e.g., *Discodorididae branneri*). The largest paratype (ZMA Moll. 3.63.021) was dissected for the present study. The second paratype (labeled paratype #2 in the jar) does not seem to be part of *Tayuva* but could not be identified, mainly because its reproductive system is in poor condition and because it could not be determine whether or not its dorsal notum bears caryophyllidia.

Type material condition (*ketos gila*).— One specimen (22/13 mm) has a complete dorsal notum and a complete pedal sole, but all its internal organs are missing. The second specimen (16/6 mm) is completely destroyed (pieces of the dorsal notum, the foot, and the digestive gland remain). No slides were found at the MZSP.

Additional material dissected.— **Caribbean Sea**, Virgin Islands, St. Thomas, [no collecting date], one specimen 60/35 (#4) mm preserved, leg. Riise, identified as *Peltodoris crucis* by Bergh (ZMUC, no catalogue number) [this specimen is designated here a as paralectotype of *crucis* Ørsted *in* Mörch, 1863:33; it is one of the four type specimens of *crucis*]; Caribbean Sea, Cayman Islands, Grand Cayman Island, off Southwest Point, outside of Sand Cay, 22 meters depth, night dive, 7 May 1991, two specimens 20/10 (#1) and 20/10 (#2) mm preserved, leg. T. M. Gosliner, identified as *Discodoris evelinae* by T. M. Gosliner (CASIZ 077318).

Distribution.— Caribbean Sea: Curaçao (Marcus and Marcus, 1963, 1970a, type locality of *hummelincki* and *ketos gila*), Aruba (Marcus and Marcus, 1963, as *hummelincki*), Cayman Islands (present study), St. Thomas, Virgin Islands (as *crucis*, see this species). The subspecies *hummelincki igla*, found off the Atlantic coast of Colombia (Marcus and Marcus, 1967b; Marcus, 1976a), does not belong to *Tayuva*. It is treated as a separate taxa (see below).

WWW.— A specimen identified as *Discodoris evelinae* and photographed by Ross W. Gundersen from St Ann's Bay, Jamaica, under bed of *Thalassia*, at 2 meters depth, October 9, 2003, probably is part of *lilacina*, although this would need to be verified through dissection.

Occurence.— In the Caribbean Sea, *lilacina* is only known from eight specimens from Curaçao, two from Aruba, two from the Cayman Islands, and one from the Virgin Islands (St. Thomas). However, the Caribbean Sea has been poorly sampled, and it might be more common.

Habitat.— The specimens collected from Piscadera Baai, Curaçao (i.e., a paratype of *hum-*

melincki and the two syntypes of *ketos gila*) were collected under stones.

LITERATURE.— Eveline and Ernst Marcus provided information about the external morphology and the anatomy of *lilacina* in the Caribbean in two contributions (Marcus and Marcus, 1963, as *hummelincki*; Marcus and Marcus, 1970a, as *ketos gila*). No color picture was published prior to the present study. Marcus and Marcus (1967a) briefly compared *lilacina* (as *hummelincki*) to *greeleyi*.

REMARKS ON THE ORIGINAL DESCRIPTION (*hummelincki*, Fig. 54-55, 56E, 61A).— The color of living animals was described as: "grayish-pinkish with deep-lying clusters of brown chromatophores under white, blunt papillae stiffened by spicules." The ventral surface is marked with brown spots of different sizes. Currently, the holotype is creamish, but the brown spots on the dorsal notum can still be observed. The largest paratype (labeled #1 in the jar), dissected for the present study, is homogeneously creamish: the darker spots on the dorsal surface are faded. The second paratype (labeled #2 in the jar), not dissected for the present study, is homogeneously creamish. This specimen actually looks different from the two other types. Its notum may bear caryophyllidia, in which case it would not belong to *Tayuva*, although this is unclear. Marcus and Marcus mentioned in some preserved specimens the presence of "two not quite regular rows [of brown spots], beginning behind the rhinophores and meeting behind the gills." This pattern can be found in *lilacina* specimens from other regions as well as in other species, especially the young specimens of *fragilis*. The maximum length of preserved specimens mentioned by the Marcus (50 mm) most likely refers to the 45 mm long preserved paratype dissected here (labeled paratype #1). The dorsal "papillae" are not caryophyllidia, at least in the holotype and the paratype #1. The Marcus described some general features shared by all *Discodorididae* (e.g., digitiform oral tentacles, bilabiate anterior foot with the superior lip notched…) as well as some general morphological and anatomical features for this species (e.g., 20 rhinophoral lamellae, presence of six tripinnate branchial plumes, absence of two symmetrical jaws). Two radular formulae were provided: 25 × (32-0-32) for a 27 mm long preserved specimen and 16 × (22-0-22) in a 12 mm long preserved specimen. According to Marcus and Marcus, the jaws are absent. However, there are two strong jaw plates in the paratype dissected here. Eveline and Ernst Marcus described carefully the anatomy of the reproductive system. In particular, they mentioned the presence of two critical characters. First, the wide, folded proximal part of the deferent duct (see their figure 34): "The wall of the prostate is folded and glandular; the whole organ is distinctly set off from the next, whitish section, a wide, folded and thin-walled efferent duct which narrows to the muscular, terminal part of the male duct." Second, the presence of a muscular wall in the distal part of the reproductive system: according to their drawing, this wall is placed laterally, as often observed. The absence of jaws in the original description of *hummelincki* is important because Marcus and Marcus consequently placed *hummelincki* within *Peltodoris*. It also might explain why, later, Marcus and Marcus (1967a, 1970a) were unable to see the similarity between *Peltodoris hummelincki* and *Tayuva ketos gila* (see discussion).

REMARKS ON THE ORIGINAL DESCRIPTION (*ketos gila*, 56A-C).— The color (probably preserved) was described as: "grey back with dark blotches, and white underside, sole with small dark spots. Shaft of rhinophores uniformly grey, foliations flecked." The preserved animals measured 26/14.5 and 15/6.5 mm. The tubercles (called "papillae" by the Marcus) are not caryophyllidia. The Marcus described some general features shared by all *Discodorididae* (e.g., digitiform oral tentacles, bilabiate anterior foot with the superior lip notched…) as well as some general morphological and anatomical features for this species (e.g., 20 rhinophoral lamellae, presence of six pluripinnate branchial plumes, presence of two jaw plates). Two radular formulae were provided: 22 × (32-0-32) for a 26 mm long preserved specimen, and 18 × (28-0-28) in a 15 mm long preserved specimen. The presence of "coalesced innermost teeth with irregular denticles" certainly is an anomaly, despite the fact that it was found in two specimens. Eveline and Ernst Marcus described carefully the anatomy of the reproductive system. In particular, they mentioned two important features. They drew a wide, folded proximal part of the deferent duct. They drew and described the distal muscular wall, although they interpreted it as a "thick bundle of spicules." According to their drawing, this wall is lateral and only protects one side of the distal part of the reproductive system, the vestibule formed by the deferent duct and the vagina.

Description of new specimens (Figs. 53A, 56D, 57-61).— This description is based on a 45 mm long paratype (#1) of *hummelincki* from Curaçao (ZMA Moll. 3.63.021), a 60 mm long paralectotype (#4) of *crucis* from St. Thomas, Virgin Islands, and two non-type specimens from the Cayman Islands (CASIZ 077318). In order to avoid any confusion, differences among these specimens are carefully pointed out.

Color. Living animals (CASIZ 077318) had a tan ground color with darker spots on the dorsal notum. The color of the ventral surface (hyponotum and foot) of living animals is unknown. Preserved, the specimens from the Cayman Islands are homogeneously creamish on both dorsal and ventral surfaces. The paratype of *hummelincki* is homogeneously creamish, with faded darker spots on the dorsal surface. The paralectotype of *crucis* is homogeneously whitish, with faded traces of darker spots.

External morphology. The body is oval. The length equals less than twice the width. Specimens are 60 mm (paralectotype of *crucis*), 45 mm (paratype of *hummelincki*, ZMA Moll. 3.63.021), and 20 mm (CASIZ 077318) long preserved. The foot is rounded posteriorly and anteriorly. The width of the foot equals about one third or one half of the width of the dorsal notum (in preserved specimens). The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, but not grooved. The dorsal notum bears tubercles that are not caryophyllidia. Many small holes (diameter < 10 µm) and many tufts of cilia were found on the surface of the dorsal notum, including the

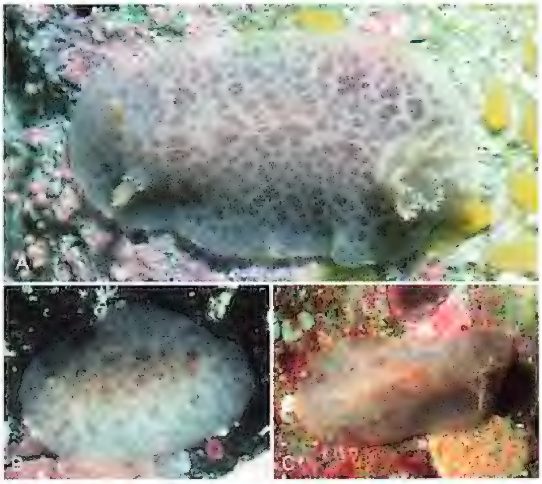

FIGURE 53. *Tayuva lilacina* (Caribbean and eastern Pacific), dorsal color. A. *Tayuva lilacina* (Caribbean), CASIZ 077318 (T.M. Gosliner).— B. *Tayuva lilacina* (eastern Pacific), CASIZ 078386 (T.M. Gosliner).— C. *Tayuva lilacina* (eastern Pacific), CASIZ 088214 (T. M. Gosliner).

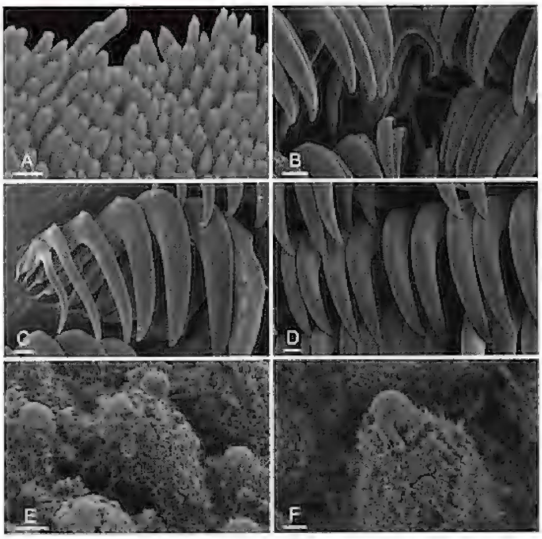

FIGURE 54. *Tayuva lilacina*, paratype of *hummelincki*, ZMA Moll. 3.63.021 (#1). A. Jaw rodlets, scale = 10 µm.— B. Innermost teeth, scale = 20 µm.— C. Outermost teeth, scale = 20 µm.— D. Median teeth, scale = 20 µm.— E. Dorsal notum, tubercles, scale = 100 µm.— F. Dorsal notum, tubercle, scale = 40 µm.

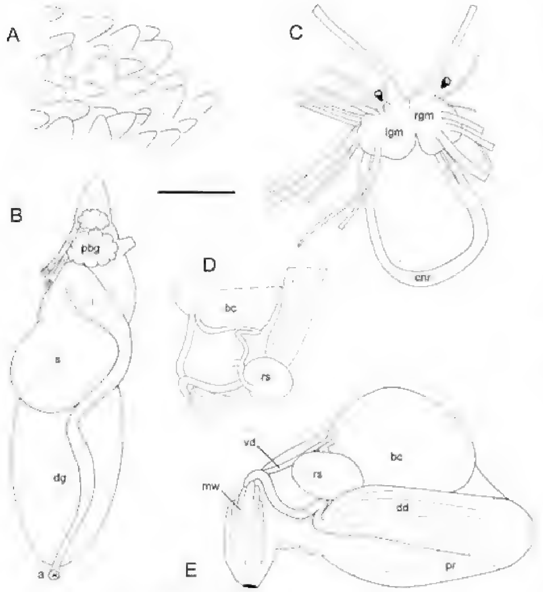

FIGURE 55. *Tayuva lilacina*, paratype of *hummelincki*, ZMA Moll. 3.63.021 (#1). A. Dorsal tubercles, scale = 1.2 mm.— B. General anatomy, scale = 17 mm.— C. Nervous system, scale = 1.2 mm.— D. Spermatic pouches, scale = 6 mm.— E. Reproductive system, scale = 3 mm.

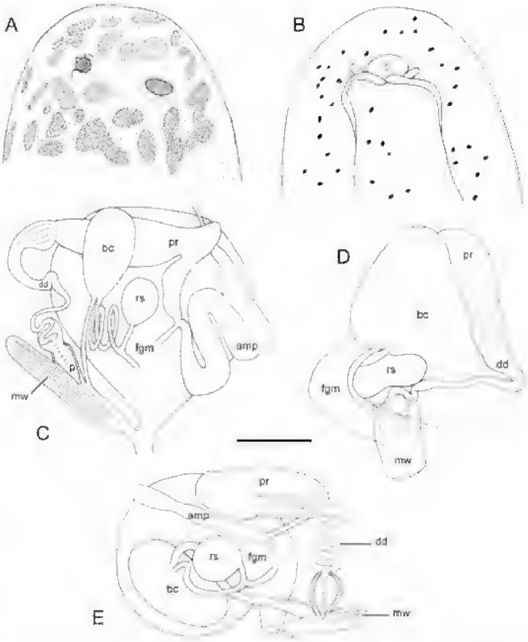

FIGURE 56. *Tayuva lilacina* (Caribbean). A. Dorsal notum, anterior view, *Tayuva ketos* gila, syntype, MZSP 43478 (#1), total width = 13 mm.— B. Ventral surface, anterior view, *Tayuva ketos gila*, syntype, MZSP 43478 (#1), total width = 13 mm.— C. Reproductive system, *Tayuva ketos gila*, after Marcus and Marcus (1970a: fig. 120).— D. Reproductive system, *Doris crucis*, paralectotype, ZMUC (#4), scale = 6 mm.— E. Reproductive system, *Peltodoris hummelincki*, after Marcus and Marcus (1963: fig. 34).

rhinophores and the gills. Some tubercles have an apex entirely covered with cilia, which makes them look like caryophyllidia without a regular crown of protruding spicules. In preserved specimens, the margins of the rhinophoral and branchial sheaths are loosely crenulate. There are six tetra- or tripinnate branchial plumes arranged in circle around the anus. The rhinophores have 25-30 (paralectotype of *crucis*), 28 (ZMA Moll. 3.63.021) and 12-15 (CASIZ 077318) lamellae.

Digestive system. The stomach is large, free, on top of the left anterior side of the digestive gland. A small caecum is located on the left posterior side of the stomach (a caecum could not be observed in the paratype). The intestine is straight and dorsal. The labial cuticle is armed with a pair of jaws constituted by rodlets. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. Radular formulae are: 18 × (24-0-24) in a 20 mm long specimen (CASIZ 077318 #1), 22 × (45-0-45) in a 45 mm long specimen (ZMA Moll. 3.63.021), and 28 × (50-0-50) in a 60 mm long specimen (paralectotype *crucis*). The rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the six or ten innermost teeth of which the size increases gradually and the four or six outermost ones of which the size decreases gradually. All teeth are hamate, including the outermost ones, although the base of the last outermost tooth is reduced. The teeth are not grooved and bear no denticles. However, occasionally, the outermost tooth bear one denticle (CASIZ 077318 #1), but just in a few rows (not all rows).

Nervous system. The length of the circum-esophageal nerve ring equals one (e.g., CASIZ 077318) or three (e.g., ZMA Moll. 3.63.021) times the width of the cerebro-pleural ganglia. The

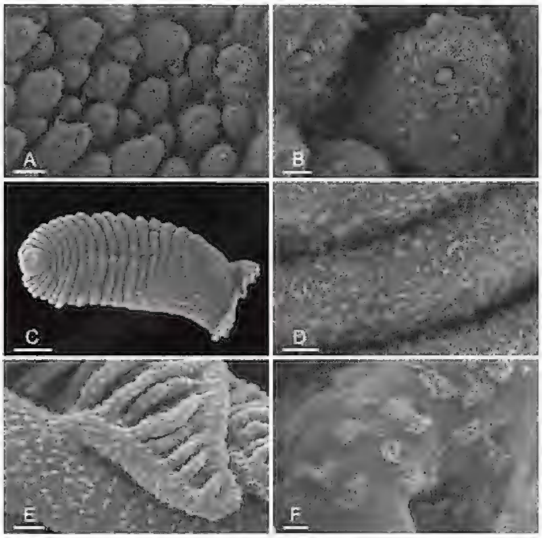

FIGURE 57. *Tayuva lilacina* (Caribbean), CASIZ 077318 (#1). A. Dorsal notum, scale = 100 µm.— B. Dorsal notum, scale = 20 µm.— C. Rhinophore, scale = 200 µm.— D. Rhinophoral lamellae, scale = 20 µm.— E. Branchial plume, detail, scale = 60 µm.— F. Branchial plume, detail, scale = 10 µm.

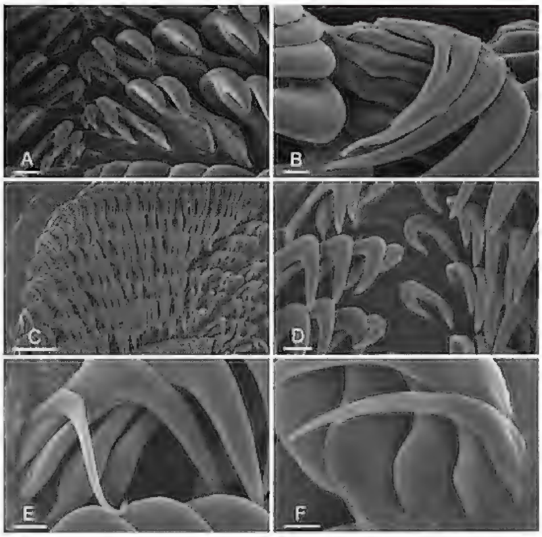

FIGURE 58. *Tayuva lilacina* (Caribbean), radula. A. Innermost teeth, CASIZ 077318 (#1), scale = 20 µm.— B. Outermost teeth, CASIZ 077318 (#1), scale = 10 µm.— C. Left rows, CASIZ 077318 (#2), scale = 100 µm.— D. Innermost teeth, CASIZ 077318 (#2), scale = 20 µm.— E. Outermost teeth, CASIZ 077318 (#2), scale = 10 µm.— F. Outermost teeth, CASIZ 077318 (#2), scale = 10 µm.

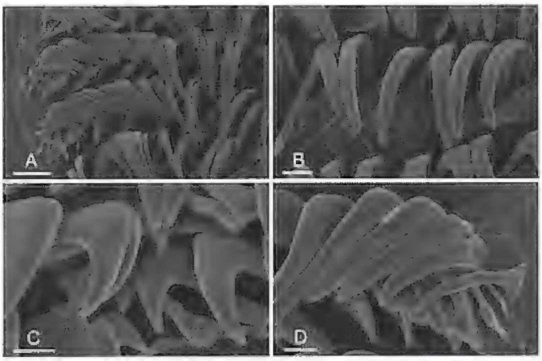

FIGURE 59. *Tayuva lilacina* (Caribbean), radula, paralectotype of crucis. A. Outermost and median teeth, scale = 100 µm.— B. Median teeth, scale = 40 µm.— C. Innermost teeth, scale = 20 µm.— D. Innermost teeth, scale = 30 µm.

cerebral and pleural are fused, and may (e.g., CASIZ 077318) or may not (e.g., ZMA Moll. 3.63.021) be separate from the pedal ganglia. Their surface is smooth.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The reproductive system of one specimen from the Cayman Islands was present but largely immature (CASIZ 077318 #2). The ampulla makes several tight loops. The division between male and female ducts (hidden within the female gland mass) could not be seen by dissection. The prostate is divided in two parts, a proximal whitish part and a distal yellowish-orange part. The deferent duct is short and straight. More importantly, its proximal part, near the prostate, is wide (much wider than usual), and folded longitudinally; these folds are internal but clearly distinct externally. The deferent duct ends in a distinct penis that does not correspond to the evaginable distal part of the deferent duct. It presents a basal part that is more or less cylindrical and that bears an elongated, narrower apical tail. The apical tail is longer if the basal part is shorter (ZMA Moll. 3.63.021: paralectotype of *crucis*) and, reciprocally, the apical tail is shorter if the basal part is longer (CASIZ 077318 #1). The maximum length found was 1.4 mm (paralectotype of *crucis*). The vaginal duct is short, straight. The deferent duct and the vaginal duct join together and form a vestibule that is separate from the female duct. More importantly, a strong muscular wall protects the distal area of the reproductive system, in particular the vestibule formed by the penial sheath and the vaginal duct. The short fertilization duct is convoluted (with one or two loops). The connection between the fertilization duct and the female gland mass is marked by a distinct duct. The duct of the receptaculum seminis is short but distinct too. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is hidden by the receptaculum seminis. The sizes of the two spermatic pouches can be more or less equal (CASIZ 077318 #1); the size of bursa copulatrix can equal five or six times that of the receptaculum seminis (ZMA Moll. 3.63.021); or the bursa can be much bigger (almost ten times) than the receptaculum seminis (paralectotype of *crucis*). Both spermatic pouches are spherical-ovate, although the receptaculum may be more elongated (CASIZ 077318 #1; paralectotype of *crucis*).

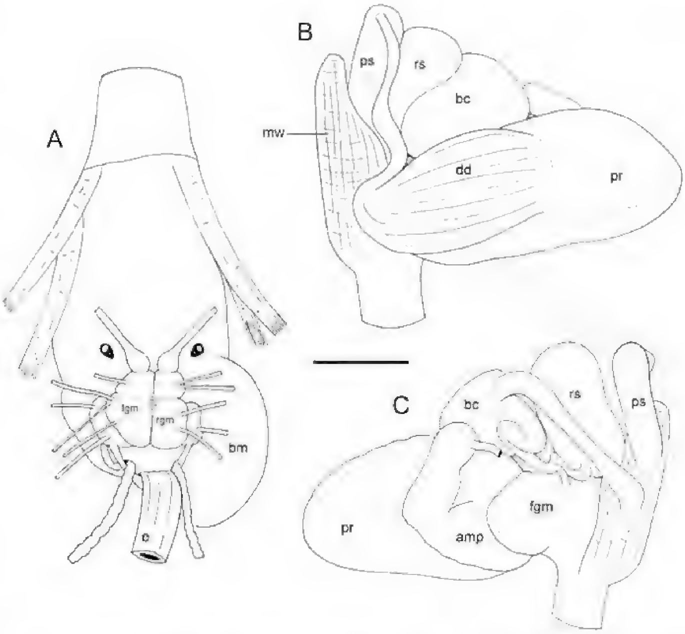

FIGURE 60. *Tayuva lilacina* (Caribbean), CASIZ 077318 (#1). A. General anatomy, scale = 1.2 mm.— B. Reproductive system, scale = 0.8 mm.— C. Reproductive system, scale = 0.8 mm.

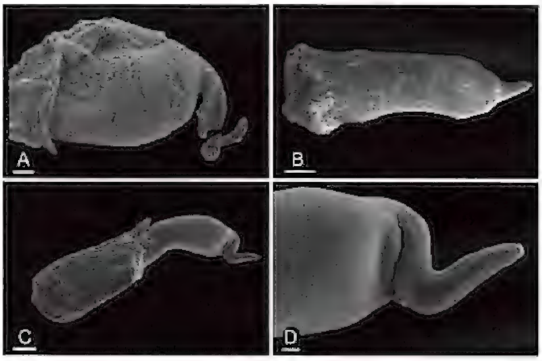

FIGURE 61. *Tayuva lilacina* (Caribbean), penis. A. Paratype, ZMA Moll. 3.63.021 (#1), scale = 100 µm.— B. Paralectotype of crucis, scale = 200 µm.— C. CASIZ 077318 (#1), scale = 100 µm.— D. CASIZ 077318 (#1), scale = 20 µm.

INFRA-SPECIFIC CHARACTER VARIATION (CARIBBEAN REGION).— Infra-specific character variation could not be addressed thoroughly because only four individuals were available. However, the differences found in the radular formulae or the size of the different parts of the reproductive system fit well with the variation observed among *lilacina* specimens from other regions (see below). Anatomical and morphological data available in the literature also are compatible with the description provided here. The largest preserved animal known is 60 mm long, which should correspond to an 85 mm length, alive. Overall, the number of rows varies from 16 (for 22 teeth per half row) to 28 (for 50 teeth per half row), and the number of teeth per half row varies from 22 (for 16 rows) to 50 (for 28 rows). Both of those numbers vary depending on the size of the individual.

DIAGNOSTIC FEATURES.— The specimens redescribed here are part of the widely-distributed species *Tayuva lilacina* because they can hardly be distinguished morphologically or anatomically from animals found in other regions (see below). In the Caribbean, *lilacina* may be easily confused with *Discodorididae branneri* (the valid name for *Discodoris evelinae*). However, these two species, which look alike externally (at least based on the limited information available), have a completely distinct reproductive system: *branneri* has a penis entirely covered with large spines (see this species).

Discussion.— The names *hummelicki* and *ketos gila* clearly refer to the same species. As a matter of fact, the two original descriptions are so similar that it is hard to understand that the Marcus could create two different names without thinking that they could refer to the same entity. They did not recognize that the character they thought was diagnostic of the genus-level taxon *Tayuva*, i.e., the presence of a muscular wall in the distal part of the reproductive system, was unambiguously present in the reproductive system of *hummelincki*. Also, they did not mention the existence of *hummelincki* when they created the new subspecies name *ketos gila*. The fact that these two names were placed in two different genera, *Peltodoris* and *Tayuva*, because of the supposedly absence of jaws in *hummelincki*, prevented the Marcus from considering that *ketos gila* and *hummelincki* could be synonyms. Two hypotheses can explain that the Marcus did not mention the presence of jaw plates in the original description of *hummelincki*. First, they simply missed the jaws, because the jaws were not as dark as usual and could not be seen without SEM. Second, the two specimens they dissected did not have jaws. However, it is likely that they simply missed the jaws. Indeed, confusing cases of presence/absence of jaws only occur when rodlets are difficult to observe, such as in *Discodorididae aurila* (see this species), but the jaws found in all the specimens dissected here were strong and unmistakably present. Another synonym had probably been created earlier, i.e., *Discodorididae muta*, based on specimens collected from Guadeloupe. However, the syntype of *muta*, dissected for the present study, was poorly preserved, and two critical characters of the reproductive system (the distal muscular wall and the wide, folded, proximal part of the deferent duct) could not be observed. Therefore, *muta* is regarded here as a *nomen dubium* (see *muta* for discussion). If it were to be demonstrated that the populations of *Tayuva lilacina* from the Caribbean Sea are part of a distinct species (reproductively isolated from *Tayuva* specimens from other regions, the valid name of that species would be *Tayuva hummelincki*, which is the oldest name created for a *Tayuva* species from the Caribbean.

Tayuva lilacina (Gould, 1852)

Region: Panamic eastern Pacific
Figures 53B-C, 62-79.

Tayuva ketos Marcus and Marcus, 1967a:192-194, figs 52-56.— Keen, 1971:825-826, fig. 2345.— Farmer, 1980:110.— Ferreira & Bertsch, 1975:326-327, figs 9-10.— Ballesteros, Llera and Ortea, 1985:254-256, fig. 15.— Dayrat and Gosliner 2005:205, 223. **New synonym.**

Tayuva ketos ketos Marcus and Marcus, 1970b:203. **New synonym.**

Discodoris ketos.— Valdés, 2002:569-571, figs 19-20.— Camacho-García et al., 2005:86, unnumbered figure.— Behrens and Hermosillo, 2005:70, fig. 130.

Type material.— Lectotype (USNM 678409), designated by Valdés (2002): one specimen 28/21 mm preserved length, leg. Peter Pickens, 2 November 1963. Paralectotype (USNM 753643): one specimen 50/35 mm preserved length, leg. Peter Pickens, 16 April 1965. The specimen USNM 753643 was identified as a paratype by Bertsch, probably in the 1970s or 1980s: one can read on the label "Det: H. Bertsch." However, Eveline and Ernst Marcus had not designated a holotype among the type series, therefore the two type specimens were syntypes and the recognition of a paratype was not permitted. Recently, Valdés (2002) designated the specimen USNM 678409 as the lectotype, but did not mention the existence of a "paratype." First, *ketos* had two syntypes (with the Marcus), then a paratype but no holotype (with Bertsch), and finally a lectotype and a paratype (with Valdés). The simplest solution would have been to keep both specimens as syntypes because both are uninformative. Regardless, the paratype is a paralectotype because: 1) the recognition of a 'paratype' was invalid; and 2) a lectotype was designated.

Type locality.— Norse Beach, Puerto Peñasco, Sonora, Mexico (lectotype). The locality of the paralectotype is Puerto Lobos, Sonora, Mexico.

Type material condition.— The lectotype is an empty body wall. All the organs (except the digestive gland) were removed. They are probably lost (no slide could be found). The paralectotype is also an empty body wall with no organs left inside.

Additional material dissected.— **Pacific Ocean**, Galapagos Islands, Isla Baltra, 10 September 1991, one specimen 22/14 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 078386); **Panama**, Pacific coast, Gulf Chiriqui, Uva Island, [no collecting date], one specimen 12/10 mm preserved, leg. Peter Glynn, identified as *Tayuva ketos* by K. B. Meyer (USNM 739594); Panama, Pacific Coast, Isla Montuosa, 7°27.3′N, 82°14.3′W, 13 meters depth, 15 April 1993, one specimen 37/25 mm preserved, leg. T. M. Gosliner *Tayuva ketos* by T. M. Gosliner (CASIZ 088239); Panama, Pacific Coast, Islas Secas, 2 meters depth, 22 April 1993, one specimen 29/17 mm preserved, leg. T. M. Gosliner, identified as *Tayuva ketos* by T. M. Gosliner (CASIZ 088251); Panama, Pacific Coast, Islas Secas, 15 meters depth, 22 April 1993, one specimen 10/6 mm preserved, leg. T. M. Gosliner, identified as *Tayuva ketos* by T. M. Gosliner (CASIZ 088214) [the reproductive system was immature (although the penis could be extracted)]; **Mexico**, Nayarit, Sayulita, 24 January 1975, two specimens 36/20 (#1) and 25/17 (#2) mm preserved, leg. Gary McDonald, identified as *Tayuva ketos* by T. M. Gosliner (CASIZ 069113); Mexico, Nayarit, Sayulita, 24 January 1975, four specimens 35/22 (#1), 25/20 (#2), 25/20 (#3), and 25/20 (#4) mm preserved, leg. Gary McDonald, identified as *Tayuva ketos* by T. M. Gosliner (CASIZ 069108); Mexico, Nayarit, Manzanilla, 2.6 miles North of Puerto Vallarta, March 1971, two specimens 40/25 and 35/20 mm preserved, leg. A. J. Ferreira, identified as *Tayuva ketos* by A. J. Ferreira (CASIZ 001569); Mexico, Baja California Sur, Cabo San Lucas, 13 meters depth, 3 October 1996, one specimen 35/25 mm preserved, leg. Mauricio Cortez, identified as *Tayuva ketos* by T. M. Gosliner (CASIZ 157399); Mexico, Sinaloa, Mazatlan, North of Gaviota Beach, Playa las Gaviotas, 23°13′N, 106°25′W, 1 December 1953, one specimen 40/30 mm preserved, leg. L. O. Miles, *Tayuva ketos* by T. M. Gosliner (CASIZ 081808) [several drawings and pictures published by Valdés (2002) are supposed to represent the specimen CASIZ 081808 but this specimen had not been dissected prior to the present study; these figures actually represent the specimen CASIZ 072843, the only other specimen cited by Valdés as additional material]; Mexico, Gulf of California, Sinaloa, Mazatlan, 9 January 1959, two specimens 47/33 and 35/20 mm preserved, leg. L. O. Miles, identified as *Tayuva ketos* by T. M. Gosliner (CASIZ 074630) [the large specimen was dissected prior to the present study; the buccal mass was missing; the reproductive system was largely destroyed, no penis could be extracted]; Mexico, Baja California Sur, Gulf of California, North of La Paz, Puerto Ballandra Bay, 4 October 1960, two specimens 40/30 and 40/25 mm preserved, leg. A. G. Smith, identified as *Tayuva ketos* by T. M. Gosliner (CASIZ 004291); Mexico, Baja California Sur, Chileno Bay, 3 meters depth, 20 January 1984, one specimen 35/20 mm preserved, leg. T. M. Gosliner, identified as *Tayuva ketos* by T. M. Gosliner (CASIZ 073165); Mexico, Sonora, Puerto Peñasco, 18 July 1966, one specimen 26/11 mm preserved, leg. Mary Anne Hill, identified as *Tayuva ketos ketos* by Eveline and Ernst Marcus (USNM 753638) [this specimen was described by Eveline and Ernst Marcus (1970d), and only an empty body wall remains]; Mexico, Baja California Sur, South side of Pulmo Point, 7 meters depth, 22 January 1984, one specimen 23/15 mm preserved, leg. H. Bertsch and L. Aguilar, identified as *Tayuva ketos* by T. M. Gosliner (CASIZ 071415); Mexico, Baja California Sur, Las Cruces, 1 to 2 meters depth, 25 January 1984, one specimen 32/22 mm preserved, leg. T. M. Gosliner, identified as *Tayuva ketos* by T. M. Gosliner (CASIZ 072843) [this specimen was dissected prior to the present study; it likely is the specimen that Valdés (2002) dissected and represented with an erroneous catalogue number, i.e., CASIZ 081808; the buccal mass was missing and the distal part of the reproductive system was destroyed].

Distribution.— Eastern Pacific, Panamic region: Mexico (Marcus and Marcus 1967a, 1970b; Ferreira and Bertsch 1975; Ballesteros et al. 1985; Valdés 2002; present study), Panama (present study), Galapagos Islands (Dayrat and Gosliner 2005; present study). The northernmost Mexican locality is currently Puerto Peñasco, at the northern end of the Gulf of California. So far, *lilacina* (as *ketos*) has not been recorded from the Pacific coast of Baja, although it is present at the southern tip of Baja California (e.g., CASIZ 073165, East of Cabo San lucas) and in the Gulf of California. Also, a color picture published by Valdés (2002, fig. 4E, as *Discodoris ketos*) suggests that the species might be present in Costa Rica too, which makes sense given its presence in Mexico and Panama. However, the photographed specimen could not be found at the CAS (Valdés did not include this specimen in his list of material examined either). Finally, the specimens identified as *Tayuva ketos* by Ballesteros and co-authors (1985) from Isla Isabel, Nayarit, Mexico, probably are the specimens that Ortea and co-authors (1981) originally identified as *Sebadoris fragilis*.

Occurence.— A reasonable number of specimens have been collected from the Pacific coast of Mexico. However, it seems to be less common from other regions, such as Panama and the Galapagos Islands, which could be due to fewer collecting efforts.

Habitat.— Boulders and cobbles on gravel (CASIZ 074630), under turnable rock, rock and sand bottom (CASIZ 072843), rock and coral (CASIZ 073165), loose basaltic rubble (CASIZ 071415).

Literature.— Several authors described the external morphology (Marcus and Marcus 1967a, 1970b; Ballesteros et al. 1985; Valdés 2002). No picture of a live animal has been published, accompanied with a description of the internal anatomy (a picture of a specimen from Costa-Rica was published by Valdés, but its identification could not be verified with internal anatomy; and the picture published by Camacho-García and co-authors was not accompanied by a dissection). The dorsal "color" is then largely known from a black-and-white drawing from the original description. Several authors published some information about the internal characters, especially the radula (Marcus and Marcus 1967a, 1970b; Ballesteros et al. 1985; Valdés 2002). Two representations of the reproductive system have been published (Marcus and Marcus 1967a; Valdés 2002). Keen (1971) simply reproduced the Marcus' data. Finally, individual character variation was not discussed prior to the present study.

Remarks on the original description (Fig. 62).— Based on a photograph, Eveline and Ernst Marcus described the dorsal color as follows: "The notum brown blotches on a whitish ground and between them some brown papillae. These are more numerous towards the sides where the botches are smaller." Currently, the color of the lectotype is grayish with faded light spots on the dorsal surface, and whitish on the ventral surface. The ventral surface of the paralectotype is dirty gray; its dorsal side is grayish with darker brown spots. The "papillae" are tubercles that are not caryophyllidia. The Marcus described some general features shared by all discodorids (e.g., digitiform oral tentacles, bilabiate anterior foot with the superior lip notched…) as well as some morphological and anatomical features for this species (e.g., 24 rhinophoral lamellae, presence of six pluripinnate branchial plumes, presence of two symmetrical jaws). The radular formulae of the two type specimens are: 24 × (38-0-38) for the specimen 47 mm long alive, and 30 mm long preserved (USNM 678409), and 29 × (41-0-41) for a specimen 50 mm long preserved (USNM

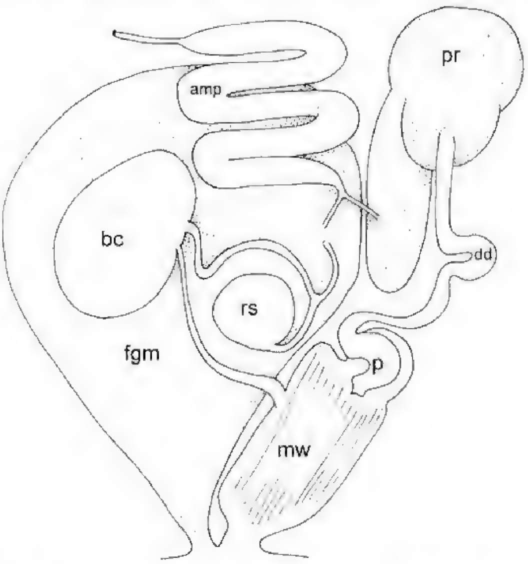

Figure 62. *Tayuva lilacina* (eastern Pacific). *Tayuva ketos*, after Marcus and Marcus (1967a: fig. 56).

753643). More importantly, the Marcus described carefully the anatomy of the reproductive system. In particular, they mentioned the presence of a "vestibular wall [that] is stiffened by a layer of longitudinal spicules, 3 mm in length and 10 µm in diameter." Although the term "spicules" was inappropriate, the vestibular wall is definitely peculiar: it is more or less entirely embedded within a strong muscular wall. As a matter of fact, based on this feature, the Marcus created a new genus name, *Tayuva*, to emphasize the difference between *Tayuva* and *Discodoris*. The deferent duct illustrated by the Marcus was as usual, i.e., narrow in its proximal part. Finally, note that the Marcus illustrated a distinct cylindrical papilla with a short pointed apex.

Description of new specimens (Figs 53B-C, 63-79).— *Color*. Two color pictures were available, one for a specimen collected from Panama (CASIZ 088214) and one for the Galapagos specimen (CASIZ 078386). The ground color is light tan-grey, with darker brown spots. The latter are irregularly arranged; their size and their darkness vary. The color of the ventral surface of living animals is unknown. The ground color of the preserved specimens (both on the ventral and the dorsal surface) is whitish-grayish. Some preserved specimens have no darker spots or dots (e.g., CASIZ 078283, CASIZ 088214). Some bear some well preserved dark brown spots on the dorsal surface and brown dots on the dorsal surface (e.g., USNM 753643, CASIZ 004291, CASIZ 001569, CASIZ 069108). Most specimens, however, only have faded traces of darker spots on the dorsal notum and some brown dots on the ventral surface (hyponotum and foot). The presence of two longitudinal rows of spots was not obvious in preserved specimens. Although it is difficult to generalize information about preserved specimens, it is likely that the ground color vary among specimens, as well as the distribution of darker ventral dots and dorsal spots.

External morphology. The body is oval. The length equals less than twice the width. The largest specimens were 40 mm long preserved (CASIZ 069113, CASIZ 001569, CASIZ 081808). The foot is rounded posteriorly and anteriorly. The width of the foot equals about one third or one half of the width of the dorsal notum (in preserved specimens). The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, but not grooved. The dorsal notum bears tubercles that are not caryophyllidia. Many small holes (diameter < 10 µm) and many tufts of cilia were found on the surface of the dorsal notum. In particular, many tubercles have an apex entirely covered with cilia, which makes them look like caryophyllidia without a regular crown of protruding spicules. In preserved specimens, the margins of the rhinophoral and branchial sheaths are crenulate. There are six wide tetra- or tripinnate branchial plumes arranged in circle around the anus, although there seems to be only four plumes in small specimens. The rhinophores have from 10 to 25 lamellae, depending on the size of the specimen.

Digestive system. The stomach is large, freely located on top of the left anterior side of the digestive gland. A small caecum is located on the left posterior side of the stomach. The intestine is straight and dorsal. The labial cuticle is armed with a pair of jaws constituted by rodlets. The length of the radula equals less than twice its width. The radular sac cannot be seen by a dorsal dissection. Radular formulae were: 13 × (26-0-26) in a 22 mm long specimen (CASIZ 078386), 15 × (22-0-22) in a 10 mm long specimen (CASIZ 088214), 15 × (26-0-26) in a 12 mm long specimen (USNM 739594), 18 × (34-0-34) in a 27 mm long specimen (CASIZ 071415), 20 × (32-0-32) in a 25 mm long specimen (CASIZ 069108 #2), 20 × (33-0-33) in two 35 mm long specimen (CASIZ 069108 #1; CASIZ 074630 #2), 20 × (34-0-34) in a 25 mm long specimen (CASIZ 069108 #4), 21 × (30-0-30) in a 25 mm long specimen (CASIZ 069108 #3) and in a 29 mm long specimen (CASIZ 088251), 21 × (34-0-34) in a 36 mm long specimen (CASIZ 069113 #1), 21 × (39-0-39) in a 40 mm long specimen (CASIZ 081808), 22 × (34-0-34) in a 35 mm long specimen (CASIZ 073165), 23 × (35-0-35) in a 35 mm long specimen (CASIZ 001569 #2), 24 × (33-0-33) in a 40 mm long specimen (CASIZ 004291 #2), 24 × (35-0-35) in a 37 mm long specimen (CASIZ 088239), 25 ×

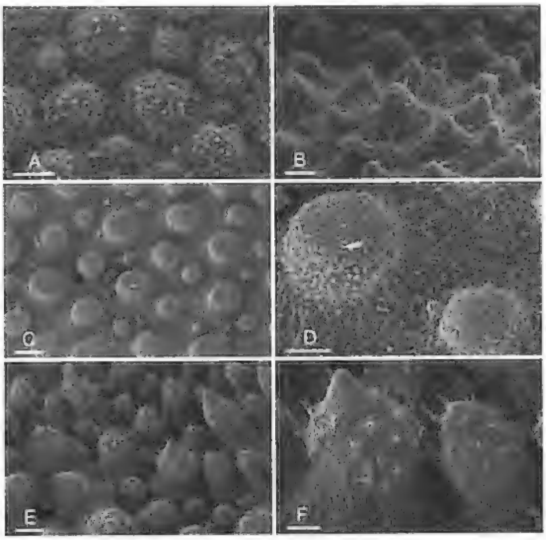

FIGURE 63. *Tayuva lilacina* (eastern Pacific), dorsal notum, tubercles. A. NMNH 753638, scale = 100 μm.— B. NMNH 753638, scale = 100 μm.— C. CASIZ 073165, scale = 200 μm.— D. CASIZ 073165, scale = 100 μm.— E. CASIZ 069113 (#1), scale = 200 μm.— F. CASIZ 069113 (#1), scale = 100 μm.

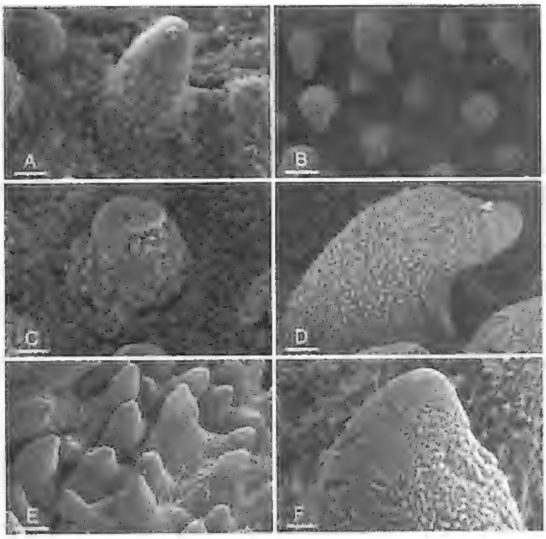

FIGURE 64. *Tayuva lilacina* (eastern Pacific), dorsal notum, tubercles. A. CASIZ 088214, scale = 40 μm.— B. CASIZ 088239, scale = 200 μm.— C. CASIZ 088239, scale = 40 μm.— D. CASIZ 088239, scale = 60 μm.— E. CASIZ 081808, scale = 200 μm.— F. CASIZ 081808, scale = 30 μm.

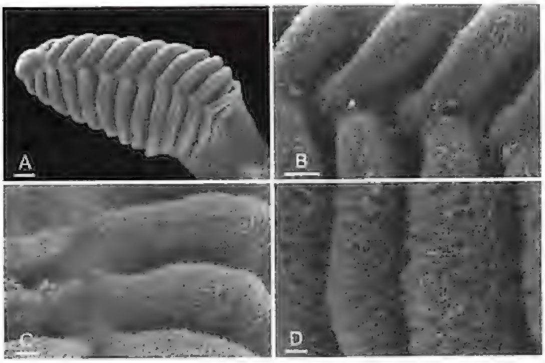

FIGURE 65. *Tayuva lilacina* (eastern Pacific), rhinophores. A. NMNH 753638, scale = 100 μm.— B. NMNH 753638, scale = 40 μm.— C. CASIZ 088214, scale = 30 μm.— D. CASIZ 069113 (#1), scale = 10 μm.

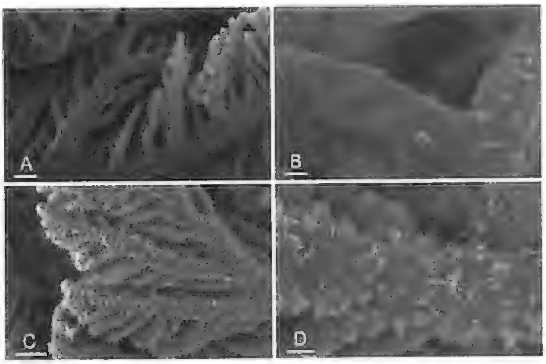

FIGURE 66. *Tayuva lilacina* (eastern Pacific), branchial plumes. A. CASIZ 088239, scale = 100 μm.— B. CASIZ 088251, scale = 20 μm.— C. CASIZ 073165, scale = 100 μm.— D. CASIZ 073165, scale = 20 μm.

(35-0-35) in a 40 mm long specimen (CASIZ 001569 #1), 26 × (40-0-40) in a 35 mm long specimen (CASIZ 157399), and 28 × (38-0-38) in a 45 mm long specimen (CASIZ 004291 #1). The rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the ten innermost teeth whose size increases gradually and the six outermost ones whose size decreases gradually. All teeth are hamate, including the outermost ones, although the base of the two outermost teeth is short. The teeth are not grooved and bear no denticles.

Nervous system. The length of the circum-esophageal nerve ring equals one to three times the width of the cerebro-pleural ganglia. The cerebral and pleural are fused. They may or may not be separate from the pedal ganglia. Their surface is smooth.

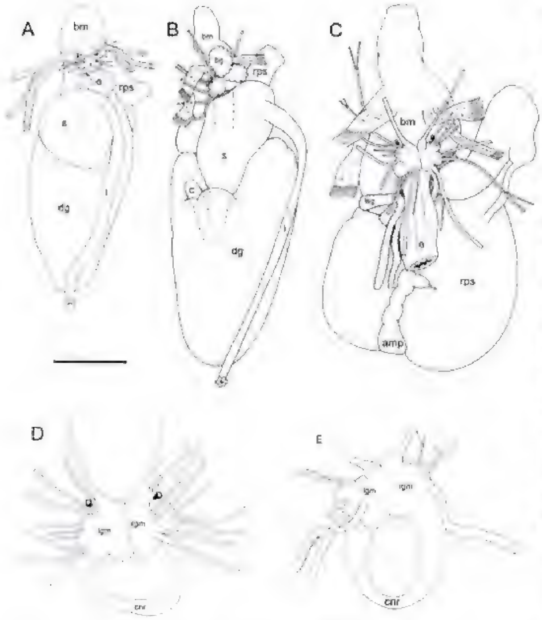

FIGURE 67. *Tayuva lilacina* (eastern Pacific), general anatomy and nervous system. A. CASIZ 088239, scale = 7.5 mm.— B. CASIZ 069113 (#1), scale = 5 mm.— C. CASIZ 069113 (#1), scale = 2.7 mm.— D. Nervous system, CASIZ 069113 (#1), scale = 1.3 mm.— E. Nervous system, CASIZ 069108 (#1), scale = 1.2 mm.

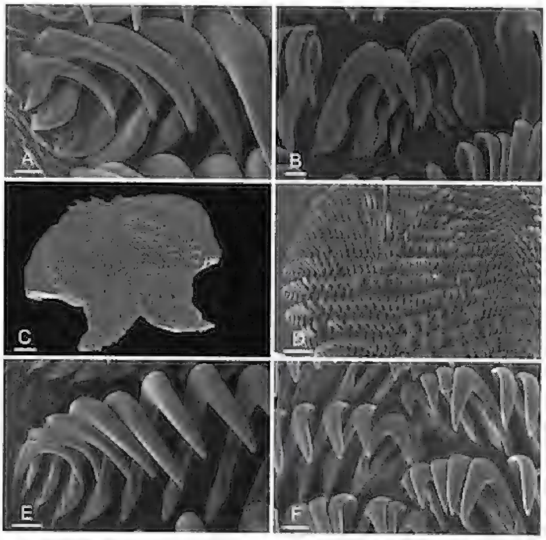

FIGURE 69. *Tayuva lilacina* (eastern Pacific), radula. A. Outermost teeth, CASIZ 001569 (#1), scale = 20 µm.— B. Innermost teeth, CASIZ 001569 (#1), scale = 20 µm.— C. CASIZ 001569 (#2), scale = 400 µm.— D. Left rows, CASIZ 001569 (#2), scale = 200 µm.— E. Outermost teeth, CASIZ 001569 (#2), scale = 40 µm.— F. Innermost teeth, CASIZ 001569 (#2), scale = 40 µm.

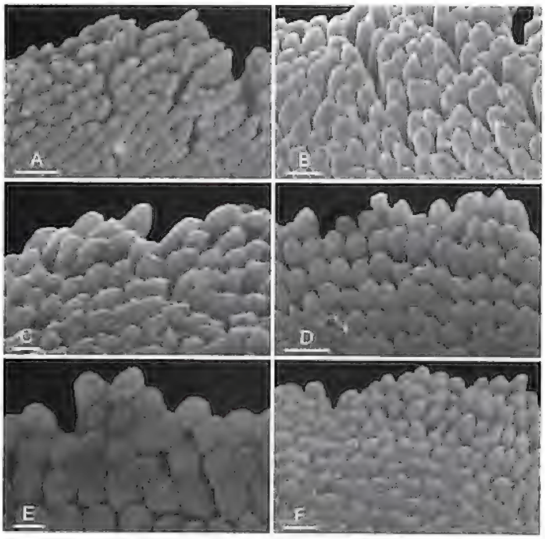

FIGURE 68. *Tayuva lilacina* (eastern Pacific), jaw rodlets. A. CASIZ 004291 (#1), scale = 20 µm.— B. CASIZ 069113 (#1), scale = 10 µm.— C. CASIZ 088214, scale = 5 µm.— D. NMNH 739594, scale = 10 µm.— E. CASIZ 088251, scale = 5 µm.— F. CASIZ 157399, scale = 10 µm.

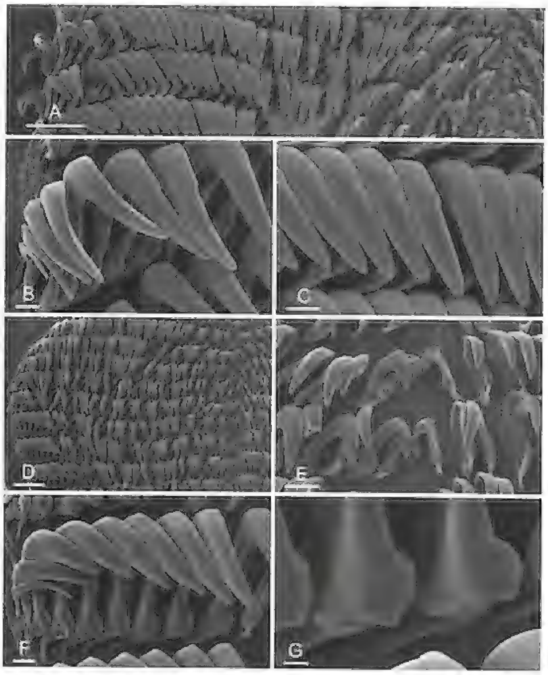

FIGURE 70. *Tayuva lilacina* (eastern Pacific), radula. A. Left rows, CASIZ 004291 (#1), scale = 200 µm.— B. Outermost teeth, CASIZ 004291 (#1), scale = 30 µm.— C. Median teeth, CASIZ 004291 (#1), scale = 40 µm.— D. Left rows, CASIZ 004291 (#2), scale = 200 µm.— E. Innermost teeth, CASIZ 004291 (#2), scale = 60 µm.— F. Outermost teeth, CASIZ 004291 (#2), scale = 30 µm.— G. Tooth base, detail, CASIZ 004291 (#2), scale = 10 µm.

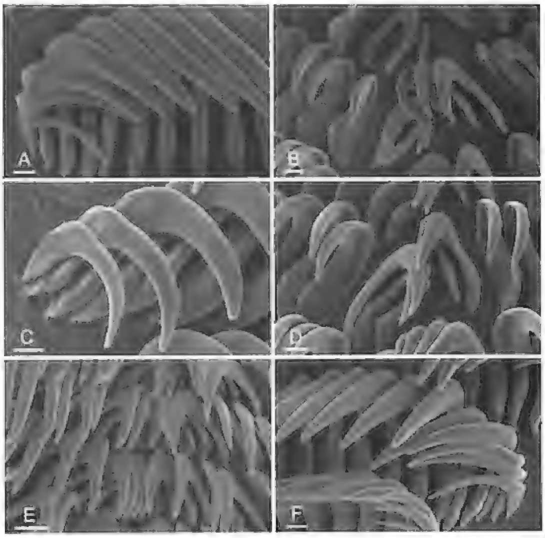

FIGURE 71. *Tayuva lilacina* (eastern Pacific), radula. A. Outermost teeth, CASIZ 069108 (#1), scale = 20 µm.— B. Innermost teeth, CASIZ 069108 (#1), scale = 20 µm.— C. Outermost teeth, CASIZ 069108 (#3), scale = 20 µm.— D. Innermost teeth, CASIZ 069108 (#3), scale = 20 µm.— E. Innermost teeth, CASIZ 069108 (#4), scale = 30 µm.— F. Outermost teeth, CASIZ 069108 (#4), scale = 20 µm.

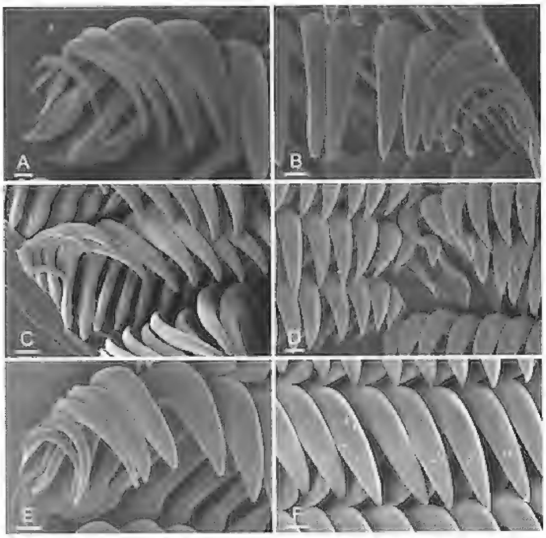

FIGURE 73. *Tayuva lilacina* (eastern Pacific), radula. A. Outermost teeth, NMNH 739594, scale = 10 µm.— B. Outermost teeth, CASIZ 073165, scale = 20 µm.— C. Outermost teeth, CASIZ 081808, scale = 30 µm.— D. Innermost teeth, CASIZ 078386, scale = 20 µm.— E. Outermost teeth, CASIZ 078386, scale = 20 µm.— F. Median teeth, CASIZ 078386, scale = 20 µm.

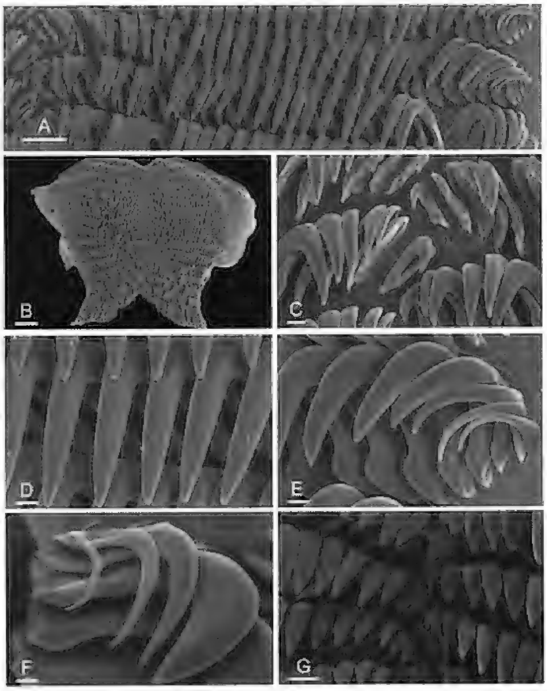

FIGURE 72. *Tayuva lilacina* (eastern Pacific), radula. A. Left rows, CASIZ 071415, scale = 100 µm.— B. CASIZ 071415, scale = 300 µm.— C. Innermost teeth, CASIZ 071415, scale = 20 µm.— D. Median teeth, CASIZ 071415, scale = 20 µm.— E. Outermost teeth, CASIZ 071415, scale = 20 µm.— F. Outermost teeth, CASIZ 088214, scale = 10 µm.— G. Innermost teeth, CASIZ 088214, scale = 30 µm.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. However, it seems to be more anterior than in other species. The reproductive system of a 10 mm long specimen from Panama was immature (CASIZ 088214). The ampulla makes several tight loops, from one or two (young individuals) to eight (larger individuals) loops. The division between male and female ducts is hidden within the female gland mass and could not be seen by dissection. The flattened prostate is divided in a white, proximal part and an orange, distal part; in several specimens, the distal part contains a third part that can be pink-orange (e.g., CASIZ 074630 #2) or whitish (CASIZ 069113 #1). This third part is difficult to observe and faded (e.g., CASIZ 004291). However, in some specimens, only two parts are recognizable, a proximal whitish part and a distal light yellowish part (e.g., USNM 739594). The deferent duct is short: it can be straight or have one or two loose loops near the penial sheath. More importantly, its proximal part (which exits the prostate) is wide (much wider than usual) and folded longitudinally; the folds are internal but clearly distinct externally. Note that this feature is present in the reproductive system of small individuals (e.g., USNM 739594). Also, the proximal part of the deferent duct is folded even when it is not significantly wider than usual (e.g., CASIZ 088239). The deferent duct ends in a distinct penis that does not seem to correspond to the devaginable distal part of the deferent duct. It presents a cylindrical base with a narrower, pointed tip. Occasionally, this tip is absent (e.g., CASIZ 081808). The surface of the penis is smooth. The length of the penis globally depends on the size of the specimens: 1.7 mm (CASIZ 004291 #1), 1.4 mm (CASIZ 069108 #1, CASIZ 001569 #2), 1.3 mm (CASIZ 074630 #2, CASIZ 069113 #1, CASIZ 088251), 1.2 mm (CASIZ 001569 #1, CASIZ 069108 #2 and #3, CASIZ 069113 #2, CASIZ 073165, CASIZ 157399), 1.1 mm (CASIZ 081808), 1 mm (CASIZ 069108 #4, CASIZ 088239), 0.4 mm (CASIZ 078386), 0.3 mm (USNM 739594), and 0.25 mm (CASIZ 088214). Note that all adult, mature specimens (>25 mm long preserved) have a penis between 1 and 1.7 mm long. No penis could be observed in the 12 mm long specimen (USNM 739594). The vaginal duct and the fertilization duct are short: they are straight or loosely convoluted. The deferent duct and the vaginal duct join together and form a vestibule that remains separate from the female duct, although they seem to merge at the end. More importantly, a strong muscular wall protects the vestibule. The female duct is not protected by this muscular wall. The muscular wall can surround entirely the distal area or simply be on one side. The connection between the fertilization duct and the female gland mass is marked by a short duct. The duct of the receptaculum seminis is short but distinct. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is hidden by the receptaculum seminis. The bursa copulatrix is from two to ten (usually five to seven) times larger than the receptaculum seminis. The two spermatic pouches are spherical-ovate, although the receptaculum seminis can be more elongated. The surface of both pouches is smooth.

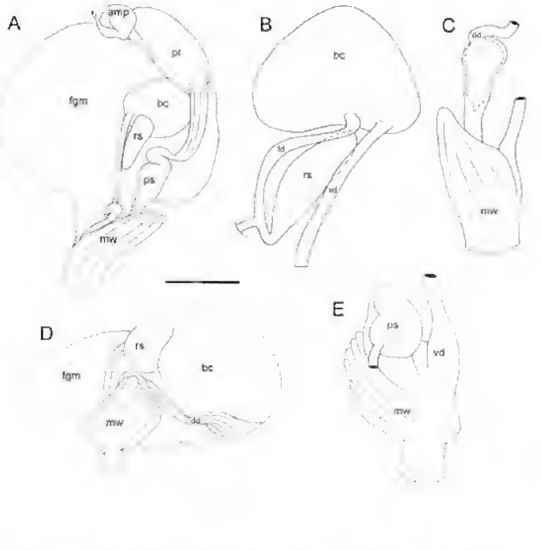

FIGURE 74. *Tayuva lilacina* (eastern Pacific), reproductive system. A. CASIZ 088239, scale = 2 mm.— B. Spermatic pouches, CASIZ 088239, scale = 1.3 mm.— C. Distal muscular wall, CASIZ 088239, scale = 1.3 mm.— D. CASIZ 081808, scale = 3 mm.— E. Distal muscular wall, CASIZ 081808, scale = 2 mm.

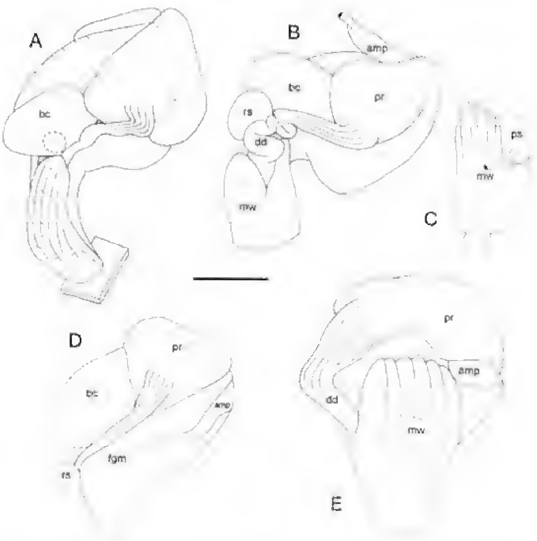

FIGURE 75. *Tayuva lilacina* (eastern Pacific), reproductive system. A. CASIZ 069113 (#1), scale = 2.6 mm.— B. CASIZ 069113 (#2), scale = 2 mm.— C. Distal muscular wall, CASIZ 074630, scale = 2 mm.— D. CASIZ 074630, scale = 3 mm.— E. Distal muscular wall, NMNH 739594, scale = 0.5 mm.

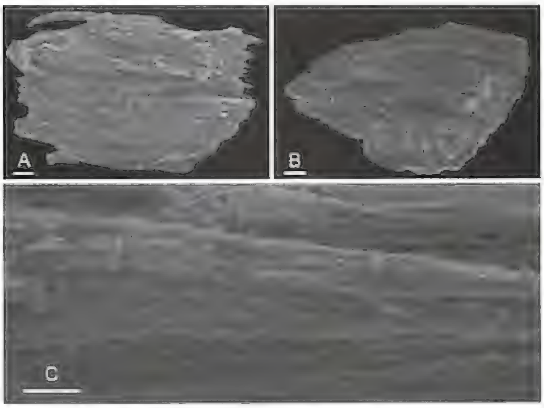

FIGURE 76. *Tayuva lilacina* (eastern Pacific), reproductive system, distal muscular wall. A. CASIZ 069108 (#2), scale = 200 µm.— B. CASIZ 069113 (#1), scale = 200 µm.— C. CASIZ 069113 (#1), scale = 40 µm.

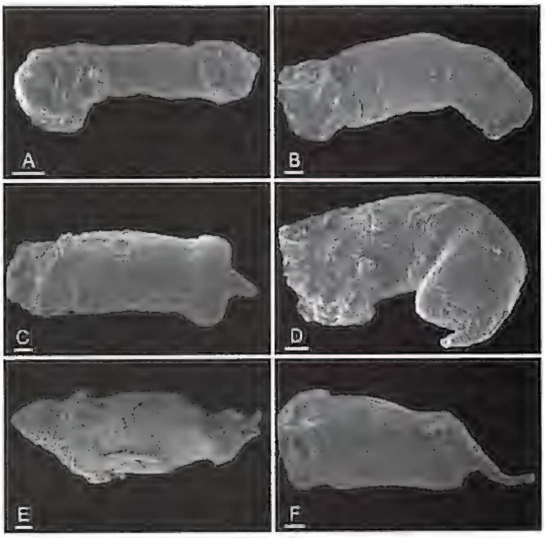

FIGURE 77. *Tayuva lilacina* (eastern Pacific), penis. A. CASIZ 069108 (#1), scale = 200 µm.— B. CASIZ 069108 (#2), scale = 100 µm.— C. CASIZ 069108 (#3), scale = 100 µm.— D. CASIZ 069108 (#4), scale = 100 µm. — E. CASIZ 069113 (#1), scale = 100 µm.— F. CASIZ 069113 (#2), scale = 100 µm.

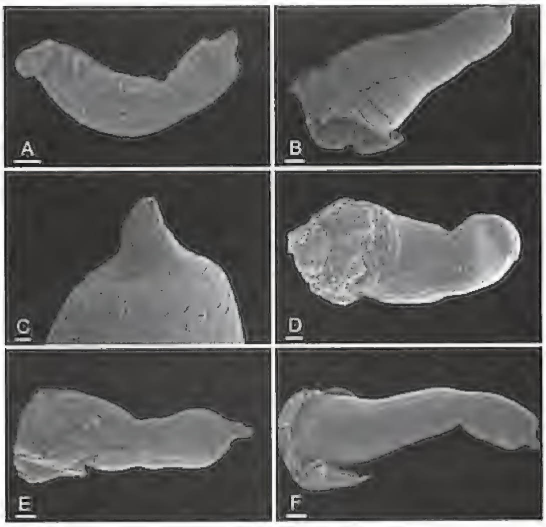

FIGURE 78. *Tayuva lilacina* (eastern Pacific), penis. A. CASIZ 001569 (#2), scale = 200 µm.— B. CASIZ 073165, scale = 100 µm.— C. CASIZ 073165, scale = 20 µm.— D. CASIZ 081808, scale = 100 µm.— E. CASIZ 088239, scale = 100 µm.— F. CASIZ 088251, scale = 100 µm.

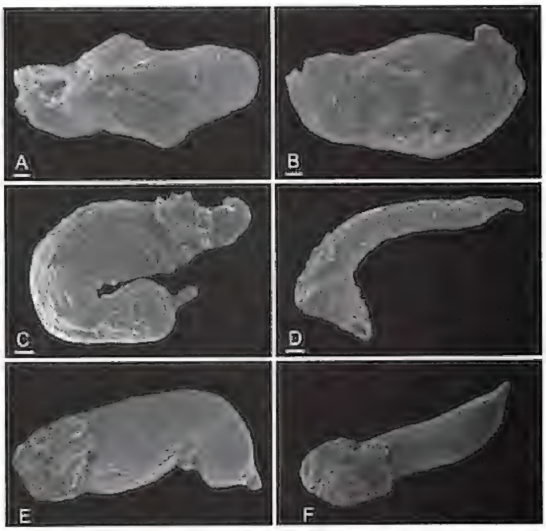

FIGURE 79. *Tayuva lilacina* (eastern Pacific), penis. A. CASIZ 088214, scale = 20 µm.— B. NMNH 739594, scale = 30 µm.— C. CASIZ 004291 (#1), scale = 100 µm.— D. CASIZ 157399, scale = 100 µm.— E. CASIZ 074630 (#2), scale = 100 µm — F. CASIZ 078386, scale = 100 µm.

INFRA-SPECIFIC CHARACTER VARIATION (EASTERN PACIFIC REGION).— Anatomical and morphological data available in the literature are largely congruent with the description provided here, except for Valdés's (2002: fig. 20B) description of the reproductive system (see discussion). The largest animal known is 50 mm long preserved (Marcus and Marcus 1967a), which approximately corresponds to a 75 mm long animal alive. Radular formulae found in the literature are (in addition to the formulae from the original descriptions): 20 × (30-0-31) in a 40 mm long specimen preserved (Ballesteros et al. 1985), 21 ×

(25-0-25) in a 25 mm long living specimen (Marcus and Marcus 1970b), 23 × (32-0-32) in a 32 mm (*not* 42 mm) long specimen preserved (Valdés 2002). Overall, so far, the number of rows varies from 13 (for 26 teeth per half row) to 29 (for 41 teeth per half row), and the number of teeth per row varies from 22 (for 15 rows) to 41 (for 29 rows). The number of teeth per row and the number of rows globally depends on the size of the specimens. The small size of the penis (0.4 mm) of the 22 mm long (preserved) individual from the Galapagos is easily explained by infra-specific variation. This does not mean that the specimens of *lilacina* in the Galapagos are not a separate species, but it simply means that we cannot regard them as a distinct species, just based on the penis size.

DIAGNOSTIC FEATURES.— The specimens redescribed here are part of the widely-distributed species *Tayuva lilacina* because they can hardly be distinguished morphologically or anatomically from animals found in other regions. In the Eastern Pacific, *lilacina* could probably not be confused. The apex of the penis of *lilacina* specimens from the Eastern Pacific has a more consistent shape than in the other regions where the length and the shape of the apex vary a great deal among specimens.

DISCUSSION.— The taxonomic history of *Tayuva ketos*, which is now synonymized with *Tayuva lilacina*, is interesting. Marcus and Marcus created the new genus *Tayuva* based on the presence of the muscular vestibular wall (which they inappropriately described as "stiffened with spicules"). Soon after, they distinguished three subspecies: *ketos ketos*; *ketos gila*, from Curaçao, and *ketos juva*, from Tubuai Islands, Polynesia, both regarded here as synonyms of *lilacina*. The fact that Marcus and Marcus interpreted all these specimens as members of the same species is interesting. In fact, specimens of *lilacina* from different regions can hardly be distinguished based on morphology. Marcus (1970) and Marcus and Marcus (1967a, 1970b, 1970c) also described repeatedly the presence of a peculiar muscular wall around the distal part of the reproductive system. Their drawings (Marcus and Marcus 1967a, fig. 56, 1970a, fig. 120, 1970c, fig. 31) clearly indicate that this wall was an additional structure, absent in other discodoridids.

Valdés (2002:565) thought that the vestibular wall described and illustrated by the Marcus was "present in all species of cryptobranch dorids," and therefore considered that *Tayuva* was a synonym of *Discodoris*. However, this wall was only found so far in *Tayuva* and no other dorids. In his drawing of the reproductive system of *ketos*, Valdés (2002: fig. 20B) did not represent a muscular wall (contrary to what is indicated in the legend of Valdés's figure 20, Valdés did not dissect the specimen CASIZ 081808, but the specimen CASIZ 072843). It could not be determined whether or not the specimen of *ketos* dissected by Valdés had a muscular wall because the distal part of the reproductive system was missing. However, the muscular wall was probably present: Valdés and Templado (2002) missed the same structure in a specimen from Lebanon that I could re-examine; also, the fact that Valdés asserted that this structure was actually present in all species cryptobranch dorids implies that he had to draw the distal part of the reproductive system exactly as usual, i.e., without the additional muscular wall; finally, the proximal part of the deferent duct is actually wide and folded, unlike what is represented by Valdés (2002: fig. 20B).

Tayuva lilacina (Gould, 1852)
Region: tropical Indo-West Pacific
Figures 80-133.

Doris lilacina Gould, 1852:297-298, plate 22, figs 392 a, b.
Discodoris lilacina.— Ono, 1999:104, fig. 167.— Suzuki, 2000:96, fig. 141.— Coleman, 2001:56, unnumbered figure.— Ono, 2004:135, fig. 273.
Tayuva lilacina.— Dayrat and Gosliner, 2005:202, 203, 209, 223.

Discodoris concinna.— Engel and van Eeken, 1962:22.— [not *concinna* Alder and Hancock, 1864].
Discodoris fragilis.— Kay and Young, 1969:187.— Kay, 1979:462, fig. 148H.— Bertsch and Johnston, 1981:40, two unnumbered figures.— Madrigal, 1999:66, unnumbered figure.— [not *fragilis* Alder and Hancock, 1864].
Discodoris palma Allan, 1933:448-449, plate 56, figs 11-12.— Allan, 1947:456-457.— Allan, 1950:222, fig. 5.— Willan and Coleman, 1984:36, fig. 111.— Marshall and Willan, 1999:74, fig. 125. **New synonym.**
Tayuva ketos juva Marcus and Marcus, 1970c:166-167, figs 31-32. **New synonym.**
Discodoris sp. A. Tonozuka, 2003:109, fig. 140.

TYPE MATERIAL (*lilacina*).— The type material of *lilacina* could not be found. It is probably lost.

TYPE MATERIAL (*palma*).— Holotype (AM C154686), by monotypy: one specimen 30/25 mm preserved, leg. G. P. Whitley, 13 February 1932. According to the label, the holotype only is a "possible holotype." It corresponds exactly to the specimen described by Allan as *palma*: Allan probably deposited it at the Australian Museum without specifying that it was the holotype of *palma*. The label also indicates that *palma* belongs to *Discodoris* or *Platydoris*. Clearly, this possible holotype of *palma* does not belong to *Platydoris*.

TYPE MATERIAL (*ketos juva*).— Holotype (USNM 576430), by monotypy: one specimen 23/12 mm preserved, leg. R. Sixberry, 1965. The radula which, according to the label, was deposited, could not be found.

TYPE LOCALITY (*lilacina*).— Honolulu, Oahu, Sandwich Islands [Hawaii].

TYPE LOCALITY (*palma*).— Sydney, Cape Banks Cruwee (Pussycat) Bay, 34°00′S, 151°14.6′E, New South Wales, Australia.

TYPE LOCALITY (*ketos juva*).— Rurutu, Tubuai Islands, Pacific Ocean.

TYPE MATERIAL CONDITION (*palma*).— The holotype was entirely dissected by Allan. The radula was removed, and is probably lost. However, the reproductive system was left inside the body wall and could be re-examined.

TYPE MATERIAL CONDITION (*ketos juva*).— The holotype was entirely dissected by Eveline and Ernst Marcus who just left the digestive gland in the body wall.

ADDITIONAL MATERIAL DISSECTED.— **South Africa**, Cape Province, Indian Ocean coast, Algoa Bay, Philip's Reef, 11 meters depth, 15 May 1984, one specimen 30/20 mm preserved, leg. W. R. Liltved, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 073468); **Tanzania**, Pwani Region, North of Dar es Salaam, off Kunduchi Beach, Mbudya Island, 3 meters depth, 27 October 1994, one specimen 30/15 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 099332); **Madagascar**, Mora Mora, opposite North Pass, near shore, patch reef, 7 meters depth, 31 March 1990, one specimen 15/10 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 073241) [the jaws and the penis were lost during SEM preparation]; **Australia**, New South Wales, Sydney, Collaroy, Long Reef, Fishermans Beach, 33°44.3′S, 151°18.6′E, 2 meters depth, 22 April 1979, two specimens 42/25 (#1) and 33/20 (#2) mm preserved, leg. I. Loch, identified as *Discodoris mauritiana* by W. B. Rudman (AM C115270) [the left side of the notum of the second specimen was not entire]; Australia, New South Wales, Batemans Bay, North Head [about 35°07′S, 150°02′ E], 28 December 1976, one specimen 22/14 mm preserved, leg. I. G. Marrow, identified as *Discodoris palma* by R. Burn (NMV F86422); Australia, New South Wales, Sydney, Botany Bay, Cape Banks, 34°00.2′S, 151°14.8′E, 10 August 1980, one specimen 40/30 mm preserved, leg. C. Finney, identified as *Discodoris* by W. B. Rudman (AM C123599); Australia, New South Wales, East of Grafton, Minnie Water, 29°46.6′S, 153°18′E, 14 May 1984, two specimens 20/12 (#1) and 20/12 (#2) mm preserved, leg. I. Bennett, identified as *Discodoris* by W. B. Rudman (AM C142251); Australia, New South Wales, Botany Bay, La Perouse, 33°59.37′S, 151°13.8′E, 13 January 1979, one specimen 40/20 mm preserved, leg. R. and A. Kuiter, identified as *Discodoris* by W. B. Rudman (AM C113759); Australia, New South Wales, Sydney, Collaroy, Long Reef, Fishermans Beach, 33°44.6′S, 151°18.6′E, 30 January 1981, one specimen 40/25 mm preserved, leg. C. Finney, identified as *Discodoris* by W. B. Rudman (AM

C126481); Australia, New South Wales, Port Stephens, Nelson Head, 32°43′S, 152°10′E, 27 October 1980, one specimen 20/10 mm preserved, leg. W. B. Rudman, identified as *Discodoris* by W. B. Rudman (AM C125186) [the penis, cylindrical with a coiled and narrower apex, was lost]; Australia, Lord Howe Island, Old Gulch, 31°30.8′S, 159°02.9′E, July 1959, one specimen 30/20 mm preserved, leg. E. Pope, identified as *Discodoris* by W. B. Rudman (AM C418422); Australia, Lord Howe Island, Neds Beach, 31°31′S, 159°04′E, 17 October 1981, one specimen 30/22 mm preserved, leg. J. Hunter and H. Woodward, identified as *Discodoris palma* by W. B. Rudman (AM C132317); Australia, Lord Howe Island, South Reef, 31°33.3′S, 159°03.9′E, 6 March 1970, one specimen 25/25 mm preserved, leg. J. Hunter and H. Woodward, identified as *Discodoris palma* by R. Burn (AM C418420); Australia, New South Wales, Woody Head, near Iluka, 29°22.09′S, 153°22.36′E, 10 March 1982, six specimens 13/8 (#1), 13/8 (#2), 12/8 (#3), 11/7 (#4), 9/6 (#5), and 9/6 (#6) mm preserved, leg. W. B. Rudman, G. A. Avern, and I. Loch, identified as *Discodoris* by W. B. Rudman (AM C132958) [no penis was found in the fifth specimen, and no reproductive system was found in the sixth specimen]; Australia, New South Wales, Arrawarra Headland, Woolgoola [probably for "Woolgoolga," about 30° S, 153° E], July 1976, one specimen 22/15 mm preserved, leg. A. Monger, determined as *Discodoris* ? *palma* by an unknown identifier (NMV F86423); Australia, New South Wales, North of Coffs Harbour, Woolgoolga headland, 30°06.6′S, 153°12.4′E, 17 March 1988, two specimens 19/12 (#1) and 18/10 (#2) mm preserved, leg. Australian Museum party, identified as *Discodoris concinna* by W. B. Rudman (AM C155707); Australia, New South Wales, Angourie Pool, 29°29′S, 153°22′E, 11 March 1982, three specimens 15/9 (#1), 13/7 (#2) and 13/7 (#3) mm preserved, leg. W. B. Rudman, I. Loch, G. A. Avern, identified as *Discodoris palma* by W. B. Rudman (AM C132978); **Indonesia**, Sulawesi, approximately 8 km North West of Ujung Pandang, Samalona Island, 1 meter depth, 10 October 1982, one specimen 20/13 mm preserved, leg. Antonio J. Ferreira, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 068283); **Papua New Guinea**, North coast, near Madang, South East side "Pig Island" [Tab Island], 17 meters depth, 24 January 1988, one specimen 18/10 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 065363); Papua New Guinea, north coast, near Madang, barrier reef between "Pig Island" [Tab Island] and Rasch Passage, reef wall, 17 Aug 1989, two specimens 11/7 (#1) and 10/6 (#2) mm preserved, M. T. Ghiselin, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 068753) [the radula and the jaws of the first specimen were lost; the penis, *lilacina*-like, was lost as well]; Papua New Guinea, north coast, Madang, near lighthouse, 8 meters depth, 22 January 1988, one specimen 12/6 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 065365); Papua New Guinea, North coast, near Madang, Daphne's Reef, between Wongat Island and Sinub Island, 13 meters depth, 7 October 1986, one specimen 10/5 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 071610) [the reproductive system was immature, although a *lilacina*-like penis was found]; Papua New Guinea, North coast, near Madang, patch reef due East of big house, 13 meters depth, 9 October 1986, one specimen 15/10 mm preserved, leg. M. T. Ghiselin, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 072829) [the penis, *lilacina*-like, was lost]; Papua New Guinea, North coast, near Madang, Daphne's Reef, between Wongat Island and Sinub Island, 13 meters depth, 7 October 1986, one specimen 8/6 mm preserved, leg. M. Ghiselin, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 072830) [the jaws were lost]; Papua New Guinea, North coast, Madang, Cement Mixer Reef (approximately WNW of Rasch Pass in line with Ruo Island), 4 meters depth, 14 June 1992, one specimen 10/7 (#1) preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 086307) [for the second and third specimen from this lot, see below the additional problematic material dissected]; **Philippines**, Luzon Island, Batangas, Dead Point, 3 meters depth, 10 May 2001, one specimen 14/8 mm preserved, leg. T. M. Gosliner, identified as *Discodoris lilacina* by T. M. Gosliner (CASIZ 156947); Philippines, Luzon, Batangas Province, Maricaban Island, Sepok Wall, 15 meters depth, 12 May 2001, one specimen 30/17 mm preserved, leg. A. Valdés, identified as *Discodoris lilacina* by T. M. Gosliner (CASIZ 158266); Philippines, Luzon Island, Batangas Province, Balayan Bay, Seafari Beach, 8 meters depth, 22 February 1995, one specimen 18/10 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 103770) [the penis, *lilacina*-like, was lost]; Philippines, Luzon Island, Batangas Province, Balayan Bay, Koala, 5 meters depth, 10 May 2001, one specimen 12/7 mm preserved, leg. Yolanda Camacho-García, identified as *Discodoris lilacina* by T. M. Gosliner (CASIZ 157146); **Marshall Islands**, Enewetak Island, lagoon side of island, 3 meters depth, 23 November 1981, one specimen 50/35 mm preserved, leg. Scott Johnson, identified as *Sebadoris nubilosa* by T. M. Gosliner (CASIZ

168913); Marshall Islands, Enewetak Island, lagoon side of island, 3 meters depth, 23 November 1981, one specimen 45/30 mm preserved, leg. Scott Johnson, identified as *Sebadoris nubilosa* by T. M. Gosliner (CASIZ 168914); **Japan**, Ryukyu Islands, Okinawa, 1.3 km ENE of Maeki-Zaki, Seragaki Beach, 26°30.4′N, 127°52.6′E, 3 meters depth, 29 April 1989, one specimen 30/17 mm preserved, leg. R. F. Bolland, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 069969) [the jaws were lost]; **Hawaii**, Oahu, Waikiki Beach, 29 May 1924, one specimen 30/17 mm preserved, leg. Charles H. Edmundson, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 031862); Hawaii, Oahu Island, Waianae, Waianae Beach Park, 9 February 1986, one specimen 28/15 (#2) mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 061455) [two additional specimens 58/38 (#1) and 25/15 (#3) mm preserved belong to this lot; however, they had been dissected prior to the present study; the reproductive system was missing in both specimens #1 and #3, and the buccal mass was missing in specimen #3]; Hawaii, Oahu Island, Kaneohe Bay, Buoy Reef, 3 meters depth, 10 September 1987, one specimen 40/25 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 071572); Hawaii, Kauai, South side of Island, Poipu Beach Park, 27 August 1992, one specimen 25/13 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 086958).

ADDITIONAL MATERIAL DISSECTED (UNCERTAIN IDENTIFICATION).— **Madagascar**, Nosy Tanikely, 11 April 1990, one specimen 8/4 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 073266) [no reproductive system was found]; **Malaysia**, Malay Peninsula, Strait of Malacca, Pulau Langkawi Island, Bay due East of Tg Chinchin, 6°25′N, 99°41′E, 18 July 1991, one specimen 11/5 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 078454) [no reproductive system was found].

ADDITIONAL PROBLEMATIC MATERIAL DISSECTED.— Here are listed some specimens with a peculiar penial morphology that differs from the penis typically found in *lilacina*.— **Papua New Guinea**, north coast, near Madang, East side of "Pig Island" [Tab Island], Barracuda Point, 25 meters depth, 19 August 1989, three specimens 20/10 (#1), 15/8 (#2), and 14/9 (#3) mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 069742); Papua New Guinea, North coast, Madang, Cement Mixer Reef (approximately WNW of Rasch Pass in line with Ruo Island), 4 meters depth, 14 June 1992, two specimens 9/6 (#2) and and 8/5 (#3) mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 086307) [another specimen (#1) from this lot is listed above with the additional material dissected]; **Philippines**, Luzon Island, Batangas, southwestern part of Calumpan Peninsula, Twin Rocks, 17 meters depth, 18 February 1992, one specimen 10/5 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 083651) [the reproductive system was present, but immature]; Philippines, Luzon Island, Batangas, South West side of Maricaban Island, Sepok Point Reef, 20 meters depth, 23 February 1992, one specimen 28/15 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 083744) [the reproductive system was fully mature but there was no penis, no distal muscular wall, and no folded proximal part of the deferent duct]; Philippines, Luzon Island, Batangas, North West side of Maricaban Island, off Layaglayag Point, Uhura Reef, 10 meters depth, 24 February 1992, one specimen 43/20 mm preserved, leg. M. Miller, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 083820) [the penis was lost]; Philippines, Luzon, Batangas Province, Maricaban Island, Devil's Point, 24 meters depth, 13 Mar 1994, one specimen 15/8 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 096341) [the reproductive system was lost].

DISTRIBUTION.— Indo-West Pacific. South Africa (present study), Tanzania (present study), possibly Red Sea (Engel and van Eeken 1962), Madagascar (present study), possibly Malaysia (present study), Indonesia (present study), Papua New Guinea (present study), Queensland (Willan and Coleman 1984, as *palma*; Marshall and Willan 1999, as *palma*), Heron Island (Marshall and Willan 1999, as *palma*), New South Wales (Allan 1933, as *palma*; Marshall and Willan 1999, as *palma*; Coleman 2001, as *lilacina*; present study), Samoa (Madrigal 1999, as *fragilis*), southern Japan (Ono 1999, 2004, as *lilacina*; Suzuki 2000, as *lilacina*; present study), Marshall Islands (present study), Tubuai Islands (Marcus and Marcus 1970c, as *ketos juva*), Hawaii (*lilacina* type locality; Kay and Young 1969, as *fragilis*; Kay 1979, as *fragilis*; Bertsch and Johnson 1981, as *fragilis*; present study).

The presence of *palma* in Western Australia (Marshall and Willan 1999, as *palma*) and Victoria (Willan and Coleman 1984, as *palma*; Marshall and Willan 1999, as *palma*) could not be verified in the context of the present study. Also, note that the specimen from NSW identified as *Discodoris palma* by Coleman (2001) is not part of *palma* (and thus *lilacina*). Finally, the identification of specimens as *Discodoris palma* by Thompson (1969, 1975) is highly questionable because those specimens have teeth and acidic secretion (Avila 1995) similar to *Geitodoris*. The identification of specimens from Singapore as *palma* (Lim and Chou 1970) is doubtful; they may have observed specimens of *murrea*, although it is uncertain.

The use of names such as *concinna*, *fragilis*, and more recently *lilacina*, has been extremely confusing in both the literature and museum collections (mainly because nobody had yet looked at the character variation among a vast number of *fragilis-lilacina*-like specimens). Therefore, are only mentioned above the few references regarded here as clear records of *lilacina*. Note that most of the non-ambiguous citations of *fragilis* or *concinna* in the literature have actually referred to *Sebadoris fragilis* (not *lilacina*), in particular in the Indian Ocean where *lilacina* is less common (at least in collections). Note, also, that *fragilis* is not known from Hawaii: so far, the Hawaiian specimens called *fragilis* are part of *lilacina*.

WWW.— The mention of the name *lilacina* on the *www* is worth discussing for several reasons. It is on the *Sea Slug Forum* that Bill Rudman (July 21, 1999) mentioned that this name that had been overlooked since its first publication by Gould in 1852. However, Rudman used this name for specimens that are part of *Sebadoris fragilis* instead of *lilacina*. Then the name *lilacina* was used to designate different entities, as far as those entities can be determined with pictures only. Some specimens identified as *lilacina* are most likely to be part of this species, although this identification would need to be confirmed through dissections, such as: the specimen photographed by David and Leanne Atkinson from Little Beach, Port Stephens, New South Wales (Sea Slug Forum, May 16, 2000, #2385); the specimen photographed by Ernest C.J. Seamark from Treasure Beach, Durban, KwaZulu Natal, South Africa, intertidal zone, December 13, 1997 (Sea Slug Forum, July 25, 1999, #1049); the 84 mm long specimen, alive, photographed by Robert F. Bolland from Onna Village, Okinawa, Japan, intertidal zone, April 21, 2000 (Okinawa Sea Slugs website, July 24, 2000); the 10 mm long specimen, alive, photographed by Jun Imamoto from Osezaki, Izu Peninsula, Suruga bay, Japan, July 20, 2002, 2 meters depth (Jun Imamoto's website); the 30 mm long specimen, alive, photographed from the Kii Peninsula, 2 meters depth, February 25, 2002 (Opisthobranchs from the Kii Peninsula website); the specimen photographed by Jeffrey Rosenfeld from Luzon Island (Sea-slugs from the Philippine Islands).

However, the name *lilacina* has also been used for specimens that are part of different entities, such as: the specimen photographed by Clay Bryce from Dampier Archipelago, Kimberley region, Northwestern Australia, probably is part of *Sebadoris fragilis* (Sea Slug Forum, May 10, 1999, #836); the 6 mm long specimen, alive, photographed by Atsushi Ono from Kerama Island, near Okinawa, Japan, intertidal zone, probably is part of *Discodorididae coerulescens* (Sea Slug Forum, May 5, 1999, #832); the 60 mm long specimen, alive, photographed by Jun Imamoto from Miura Peninsula, Sagami Bay, November 11, 2001, intertidal zone, may be a specimen that is part of *Sebadoris nubilosa*, but this identification is hypothetical (Jun Imamoto's website). Other pictures of animals identified as *lilacina* have been posted on different websites, but those doubtful identifications would need to be addressed through dissections.

OCCURRENCE.— According to Kay and Young (1969) and Bertsch and Johnson (1981), *lilacina* (which they referred to as *fragilis*) is one of the commonest of the Hawaiian dorids. This probably explains why Gould described it from Hawaii in the 1850s. It is also described as "very common at times along the New South Wales coasts" by Allan (1950). However, according to Marshall and Willan (1999), it is rare in Heron Island, and more common in temperate eastern Australian coastal waters. Also, according to Robert Bolland (see *www* above), it is rare in Okinawa (one of the three specimens he collected was dissected for the present study), but several photographs of specimens collected from Japan have been posted on the *www* recently. Globally, our current knowledge on the occurrence of *lilacina* may be biased because of different sampling efforts in different regions. However, so far, *lilacina* seems to be less common in western Indian Ocean than it is in the rest of its distribution.

HABITAT.— Under stones at low tide (Allan 1933), on sand and rubble (Coleman 2001), under rocks (AM C115270), intertidal rocks (C155707), strewn coral rubble (CASIZ 069969), under dead coral (CASIZ 168913), large boulders (CASIZ 061455).

LITERATURE.— Many authors provided general information about the color and the external morphology (Gould 1852; Allan 1933, 1947, 1950, as *palma*; Kay and Young 1969, as *fragilis*; Marcus and Marcus 1970c, as *ketos juva*; Kay 1979, as *fragilis*; Bertsch and Johnston 1981, as *fragilis*; Willan and Coleman 1984, as *palma*; Madrigal 1999, as *fragilis*; Marshall and Willan 1999, as *palma*; Ono 1999, 2004; Suzuki 2000; Coleman 2001). Radular features have been described only in three contributions (Kay and Young 1969, as *fragilis*; Allan 1933, as *palma*; Marcus and Marcus 1970c, as *ketos juva*). Marcus and Marcus (1970c) also described the reproductive system. The description of the reproductive system of specimens from Hawaii by Kay and Young (1969) probably was incomplete (see discussion). Overall, the anatomy of *lilacina* was poorly known prior to the present study. In particular, intra-specific variation of characters has never been addressed.

REMARKS ON THE ORIGINAL DESCRIPTION (*lilacina*, Fig. 80).— The original description, which is not long, is reproduced here in its entirety: "Animal rather large, somewhat prismatic, much elongated, obtuse in front, rather tapering behind. Colour lilac, tinted roseate along the middle, and mottled with rather large darker spots; there is an angular dilatation at the sides opposite the tentacles; behind these a broad, ruffled, and ochreous margin; cervical tentacles small, ochreous, club-shaped, reflexed, lamellar. Branchial star seated far back, large, wider than the body, composed of six large, trifoliate plumules, each of the folioles deeply and perhaps doubly sinuate; margin yellow. Beneath yellowish, shaded and finely spotted with lilac; foot as long as the body and two-thirds as wide, rounded at tip, and terior angles not dilated; head small, rounded, placed deep beneath the hood. Length three and one-third inches; breadth an inch and a quarter." Interestingly, Gould described specimens that are among the longest specimens known for *lilacina*. However, as discussed below (infra-specific variation), specimens from Marshall Islands and Hawaii tend to be longer than specimens from the Indian Ocean. Also, the color drawings published by Gould are informative. In particular, the drawing of the ventral color indicates that *lilacina* is not a valid name for *Sebadoris fragilis*, because the foot and the hyponotum of *fragilis* specimens have large spots, not only small dots. A lilac tint has not been reported in the literature. However, our knowledge of the color of *lilacina* has suffered a great deal from misidentifications and confusion between *fragilis* and *lilacina* in the literature. Also, interestingly, our knowledge of the color of live animals is still fairly limited.

REMARKS ON THE ORIGINAL DESCRIPTION (*palma*, Fig. 81A).— The color was described as: "very pale light grey-fawn on the dorsal surface, with darker irregular patches of speckling scattered over it, especially thick round the edge of the central dorsal portion, and becoming smaller but denser towards the margins. The central area is darker in colour than the mantle. Rhinophores are pale at the base, dark towards the middle, and have white-tipped tops. The [six] gills are pale yellow-buff with brown speckling, their stalks pale grey streaked with brown. The undersurface is pale bluish-grey, with small, dark, chocolate-coloured, irregular-sized spots scattered over it and fine minute specks between them. These spots are more dense on the mantle round the foot. Some spots are scattered over the center of the foot." The color of the preserved specimen is homogeneously creamish. The "minute pustules" described by Allan on the surface of the dorsal notum are not carophyllidia. Allan described several important characters, such as the bilabiate anterior foot with a superior lip notched, and the presence of "long and thin" oral tentacles. The labial cuticle is armed, although Allan did not specify the exact number of jaw plates (probably only two). The radula consisted of 21 rows of "numerous, long, thin, sharply curved teeth" in a 50 mm long specimen (probably alive because the preserved length is 30 mm). The intestine is straight: there is no lateral loop. Allan did not describe the reproductive system. A re-examination of the holotype provided some critical information: a muscular wall is present in the distal part of the reproductive system, and the deferent duct presents a proximal, wide, folded part, at the junction with the prostate. More importantly, there is a penial sheath hosting a penis with a coiled apex that is similar to the typical shape found in all specimens dissected here. Finally, the hermaphroditic gland is not independent from the digestive gland; the bursa copulatrix was missing; the connection between the vas deferens and the prostate is broken and cannot be determined.

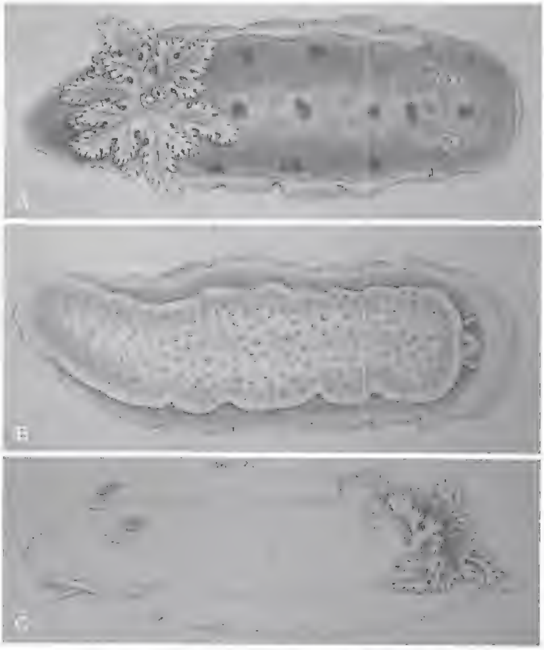

FIGURE 80. *Tayuva lilacina*, illustrations from Gould's (1852) original description. A. Dorsal view (Gould 1852: plate 22, fig. 392).— B. Ventral view (Gould 1852: plate 22, fig. 392a).— C. Lateral view (Gould 1852: plate 22, fig. 392b).

REMARKS ON THE ORIGINAL DESCRIPTION (*ketos juva*, Fig. 81B).— The original description of *ketos juva* is largely complete, except for the shape of the penis that is unclear. The color was described as follows: "The light grayish brown color is brought about by scattered melanophores which form denser blotches here and there. The shafts of the rhinophores and the gills contain dots of pigments. The hyponotum and the sole are ivory." The color of the preserved specimen is homogeneously creamish. Tubercles on surface of the dorsal notum are not carophyllidia. There are six multipinnate gills; rhinophores include 25 lamellae. The Marcus also described several important characters, such as the bilabiate anterior foot with a

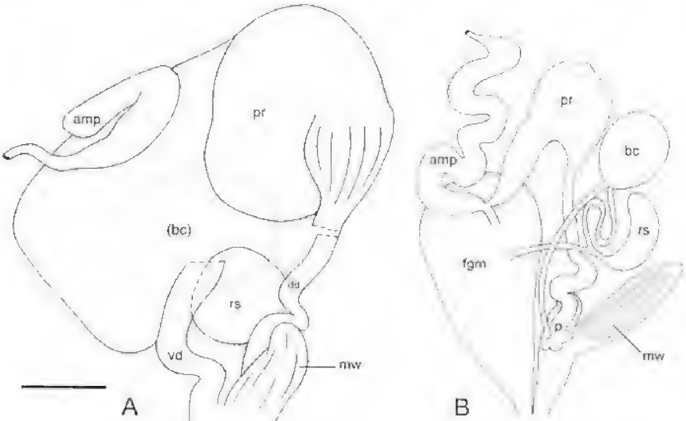

FIGURE 81. *Tayuva lilacina* (Indo-West Pacific). A. *Discodoris palma*, holotype, reproductive system, as currently preserved, scale = 1 mm.— B. *Tayuva ketos juva*, reproductive system, after Marcus and Marcus (1970c: fig. 31).

superior lip notched, and the presence of oral tentacles that are "pointed cones." The labial cuticle is armed, although Allan did not specify the exact number of jaw plates (probably only two). The radular formula was 20 × (28-0-28) in a 23 mm long preserved specimen. The Marcus carefully described a muscular wall in the distal part of the reproductive system (they call this structure a "bristle sac"). They drew a narrow deferent duct. As a matter of fact, the width of the folded proximal part of the deferent duct varies and it can easily be overlooked when it is narrow. The Marcus simply mentioned the presence of a 1 mm long and 0.2 mm thick penis, but did not provide the exact shape of its apex. Finally, the bursa copulatrix and the receptaculum are about the same size; the vaginal duct is straight; the deferent duct and the fertilization duct are loosely convoluted.

Description of new specimens (Figs. 82-123).— The problematic specimens (see above) are described separately. *Color*. Information about the color of living animals was available for several individuals dissected. The ground color of the dorsal notum is light grey-tan, with some mottled patches of brown, or spots. The number, the size, and the darkness of those spots vary among specimens. In some specimens, however, two longitudinal rows of four to six darker spots (from the rhinophores to the branchial pocket) are clearly recognizable. Also, some white pigments may be present, in particular along the median line. The gills and the rhinophores are yellowish-creamish and may bear white and light brown pigments. The ground color of the ventral surface is light grey-tan as well, with small brown dots whose number varies among individuals. However, those dots remain small, and they never form a continuous brown ring around the foot sole. The color of preserved specimens varies depending on the preservation of both ventral dots and dorsal spots. Most specimens are creamish with darker spots on the dorsal surface and darker dots on the ventral surface, provided that those spots and dots may be faded though. However, some preserved specimens are entirely creamish (e.g., CASIZ 073468, CASIZ 075365, CASIZ 072830, CASIZ 031862). Also, two longitudinal rows of spots may still be clearly recognizable in some preserved specimens (e.g., CASIZ 072829, CASIZ 103770, AM C155707, CASIZ 071610).

External morphology. The body is oval. The length equals less than twice the width. The largest specimen (CASIZ 168913, Marshall Islands) was 50 mm long, preserved, which should correspond to a 70 mm maximum length alive. Note that a maximum preserved length could be 58 mm, if the specimen CASIZ 061455 #1 is included (its reproductive system was missing and therefore its identification is not certain). Specimens that are 30 or 40 mm long (preserved) are not uncommon. However, the size of the animals seems to be correlated to geographical distribution (see below, intra-specific variation). The foot is rounded posteriorly and anteriorly. The width of the foot equals about one third or one half of the width of the dorsal notum (in preserved specimens). The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, not grooved. The dorsal notum bears tubercles that are not caryophyllidia. Many small holes (diameter < 10 µm) and many tufts of cilia were found on the surface of the dorsal notum, including the rhinophores and the gills. In well-preserved specimens, dorsal tubercles have an apex entirely covered with cilia, which makes them look like caryophyllidia without a regular crown of protruding spicules. The margins of the rhinophoral and branchial sheaths can be smooth or crenulate, depending on the preservation and on the concentration of tubercles on the margins. There are six wide tetra- or tripinnate branchial plumes arranged in circle around the anus. The number of gills is constant, and only a few exceptions were observed: a young and small specimen (CASIZ 073266) seemed to have only four plumes; two adult specimens (AM C12186, AM C132958 #2) had only four plumes (loosing accidentally branchial plumes is not rare). The rhinophores have from 10 to 25 lamellae, depending on the size of the specimen.

Digestive system. The stomach is large, free, on the left anterior side of the digestive gland. A small caecum is located on the left posterior side of the stomach; a large caecum, *fragilis*-like, was found in one specimen (NMV F86423). The intestine is straight and dorsal. The labial cuticle is armed with a pair of jaws constituted by rodlets. Note, however, that a few specimens have a smooth labial cuticle (CASIZ 065363, CASIZ 068283, CASIZ 073266, CASIZ 099332). The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. Radular formulae are given in Table 1. The maximum number of rows is 30 (in a 30 mm long, preserved, specimen – CASIZ 031862), and most specimen have a radula with less than 20 rows of teeth. The maximum number of teeth per row is 40 (in a 40 mm long, preserved, specimen – CAS IZ 071572). Most specimens have less than 30 teeth per row. The rachidian teeth are absent and the rachidian space is narrow. Exceptionally, a rachidian tooth was found in one specimen from Marshall Islands (CASIZ 168914). The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the four or eight innermost teeth of which the size increases gradually, and the four or six outermost ones of which the size decreases gradually. All teeth are hamate, including the outermost ones, although the base of the last outermost

TABLE 1. Radular formulae of specimens dissected of *Tayuva lilacina* (Gould, 1852) from the Indo-West Pacific region for the present study. The asterisk indicates specimens for which the identification is regarded here as problematic (see Text).

Cat. #	**Locality**	**Spm #**	**Size (mm)**	**Radular formulae**
CASIZ 073468	South Africa		30/20	20 ´ (24-0-24)
CASIZ 099332	Tanzania		30/15	20 ´ (27-0-27)
CASIZ 073241	Madagascar		15/10	15 ´ (21-0-21)
CASIZ 073266*	Madagascar		8/4	16 ´ (18-0-18)
AM C115270	NSW (33°44'S)	1	42/25	20 ´ (29-0-29)
AM C142251	NSW (29°46'S)	1	20/12	15 ´ (22-0-22)
AM C123599	NSW (34°00'S)		40/30	24 ´ (31-0-31)
AM C125186	NSW (32°43'S)		20/10	16 ´ (24-0-24)
AM C132317	LH Island (31°31'S)		30/22	17 ´ (27-0-27)
AM C418420	LH Island (31°33'S)		25/25	22 ´ (28-0-28)
AM C132958	NSW (29°22'S)	1	15/9	15 ´ (22-0-22)
AM C132958	NSW (29°22'S)	5	9/6	13 ´ (20-0-20)
MV F86423	NSW (*c.* 30° S)		22/15	15 ´ (25-0-25)
MV F86422	NSW (*c.* 35°07' S)		22/14	16 ´ (37-0-37)
CASIZ 068283	Indonesia		20/13	14 ´ (30-0-30)
CASIZ 065363	PNG		18/10	17 ´ (25-0-25)
CASIZ 065365	PNG		12/6	14 ´ (21-0-21)
CASIZ 069742*	PNG	1	20/10	18 ´ (26-0-26)
CASIZ 069742*	PNG	3	14/9	15 ´ (26-0-26)
CASIZ 071610	PNG		10/5	14 ´ (19-0-19)
CASIZ 072829	PNG		15/10	15 ´ (22-0-22)
CASIZ 072830	PNG		8/6	12 ´ (18-0-18)
CASIZ 086307	PNG	1	10/7	15 ´ (22-0-22)
CASIZ 086307*	PNG	2	9/6	12 ´ (18-0-18)
CASIZ 083744*	Philippines		28/15	18 ´ (37-0-37)
CASIZ 096341*	Philippines		15/8	16 ´ (19-0-19)
CASIZ 156947	Philippines		14/8	13 ´ (13-0-13)
CASIZ 158266	Philippines		30/17	20 ´ (37-0-37)
CASIZ 103770	Philippines		18/10	15 ´ (23-0-23)
CASIZ 168913	Marshall		50/35	22 ´ (31-0-31)
CASIZ 168914	Marshall		45/30	27 ´ (36-0-36)
CASIZ 069969	Japan		30/17	17 ´ (24-0-24)
CASIZ 031862	Hawaii		30/17	30 ´ (37-0-37)
CASIZ 061455	Hawaii	1	58/38	13 ´ (32-0-32)
CASIZ 061455	Hawaii	2	28/15	17 ´ (27-0-27)
CASIZ 071572	Hawaii		40/25	28 ´ (40-0-40)
CASIZ 086958	Hawaii		25/13	18 ´ (31-0-31)

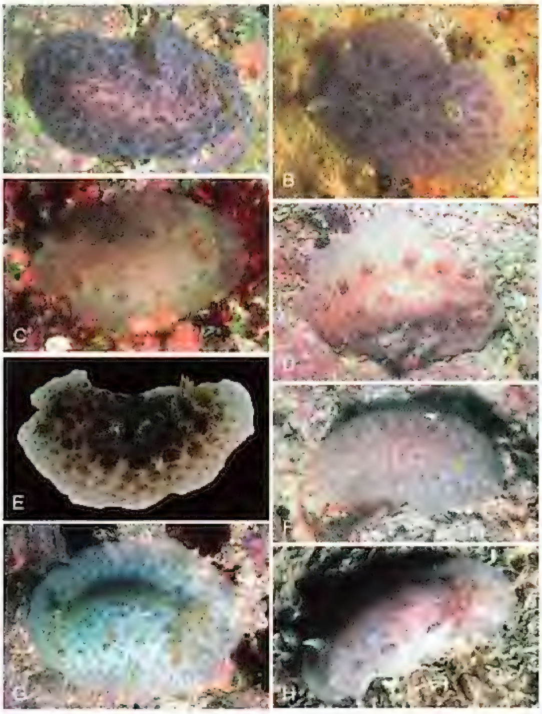

FIGURE 82. *Tayuva lilacina* (Indo-West Pacific), dorsal color. A. CASIZ 099332 (T.M. Gosliner).— B. CASIZ 157146 (Y. Camacho-García).— C. CASIZ 083651 (T.M. Gosliner).— D. CASIZ 073468 (W.R. Liltved).— E. CASIZ 069969 (R.F. Bolland).— F. CASIZ 072830 (M. Ghiselin).— G. CASIZ 061455 (T. M. Gosliner, one of three specimens).— H. Uncertain identification, CASIZ 078454 (T.M. Gosliner).

tooth can be reduced. The teeth are not grooved and bear no denticles (except for a 10 mm long specimen from Papua New Guinea – CASIZ 071610 – whose two outermost radular teeth can bear denticles, although not in all rows). No trace of spur could be found on the base of the (innermost) teeth. Also, artificially fused teeth were found in two specimens, one from the Philippines (CASIZ 156947) and one from South Africa (CASIZ 073468).

Nervous system. The length of the circum-esophageal nerve ring equals one to three times the width of the cerebro-pleural ganglia. The cerebral and pleural ganglia are fused, and may or may not be separate from the pedal ganglia. Their surface is smooth.

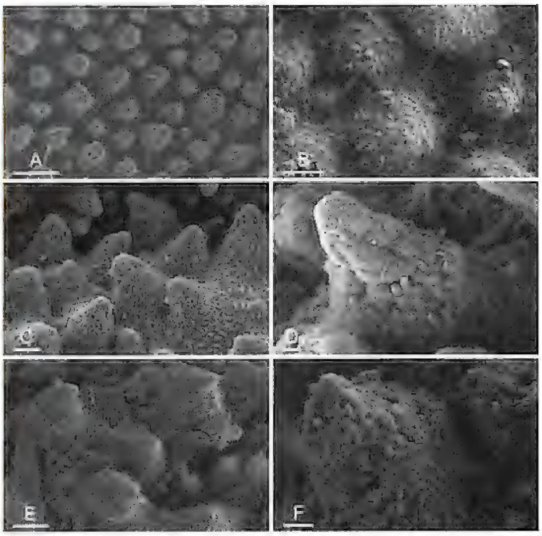

FIGURE 83. *Tayuva lilacina* (Indo-West Pacific), dorsal notum, Hawaii. A. CASIZ 061455 (#2), scale = 200 µm.— B. CASIZ 086958, scale = 100 µm.— C. CASIZ 071572, scale = 100 µm.— D. CASIZ 071572, scale = 10 µm.— E. CASIZ 031862, scale = 100 µm.— F. CASIZ 086958, scale = 40 µm.

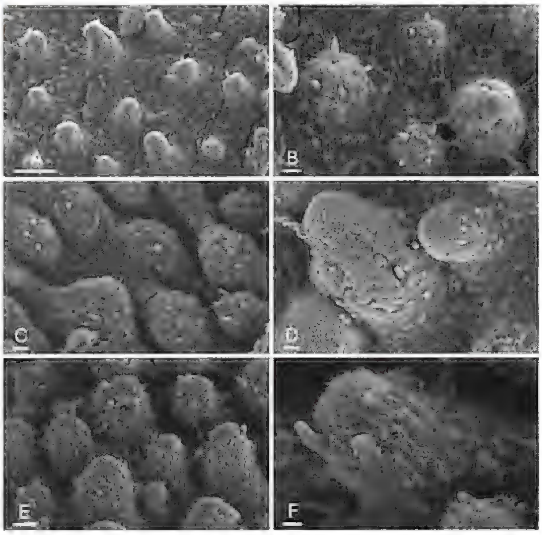

FIGURE 84. *Tayuva lilacina* (Indo-West Pacific), dorsal notum, Philippines, Indonesia, Japan. A. CASIZ 156947, scale = 100 µm.— B. CASIZ 156947, scale = 20 µm.— C. CASIZ 158266, scale = 30 µm.— D. CASIZ 158266, scale = 20 µm.— E. CASIZ 068283, scale = 40 µm.— F. CASIZ 088283, scale = 10 µm.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The hermaphroditic gland is not independent from the

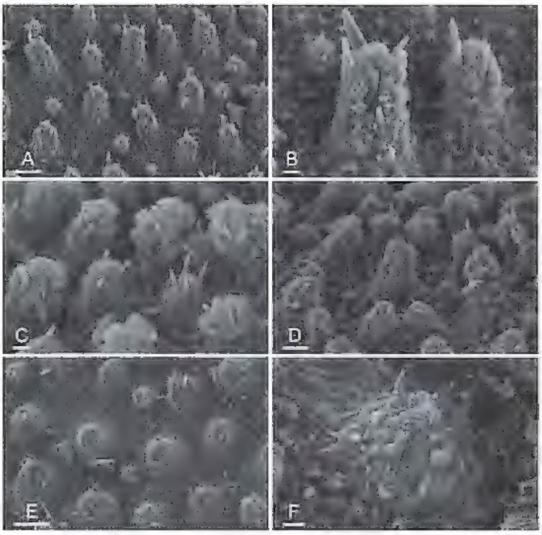

FIGURE 85. *Tayuva lilacina* (Indo-West Pacific), notum, Papua New Guinea. A. CASIZ 086307 (#1), scale = 100 µm.— B. CASIZ 086307 (#1), scale = 20 µm.— C. CASIZ 068753 (#1), scale = 20 µm.— D. CASIZ 068753 (#1), scale = 40 µm.— E. CASIZ 065363, scale = 100 µm.— F. CASIZ 065363, scale = 20 µm.

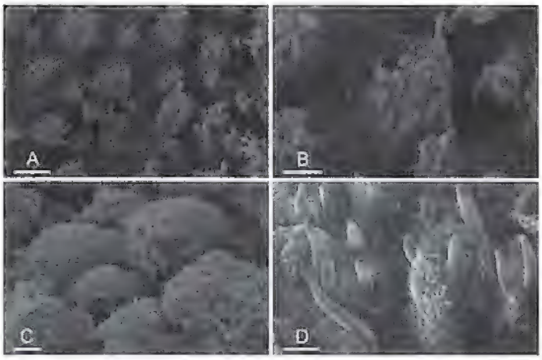

FIGURE 86. *Tayuva lilacina* (Indo-West Pacific), jaws, New South Wales. A. MV F86422, scale = 100 µm.— B. MV F86422, scale = 40 µm.— C. MV F86423, scale = 30 µm.— D. AM C155707 (#1), scale = 30 µm.

digestive gland. The ampulla makes several tight loops, usually four, but sometimes less than four or up to six. The division between male and female ducts (in the female gland mass) could not be seen by dissection. The flattened prostate is divided in three parts in most specimens. The first, proximal part is whitish. The second part is yellowish-orange. The third, distal part, which seems to be a differentiation of the second part, is whitish, yellowish, or light pinkish. In some specimens, however,

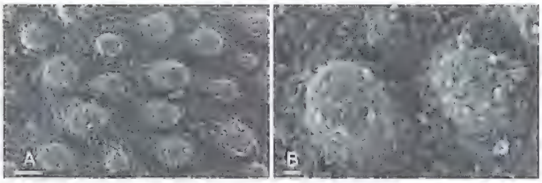

FIGURE 87. *Tayuva lilacina* (Indo-West Pacific), notum, CASIZ 099332. A. Scale = 100 µm.— B. Scale = 20 µm.

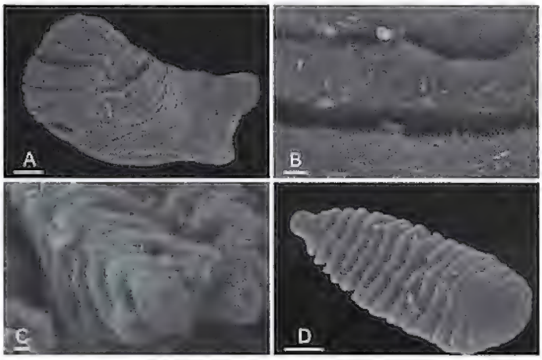

FIGURE 88. *Tayuva lilacina* (Indo-West Pacific), rhinophores and gills. A. Rhinophore, CASIZ 158266, scale = 200 µm.— B. Rhinophoral lamellae, CASIZ 158266, scale = 20 µm.— C. Branchial plume, detail, CASIZ 158266, scale = 20 µm.— D. Rhinophore, CASIZ 086307 (#1), scale = 200 µm.

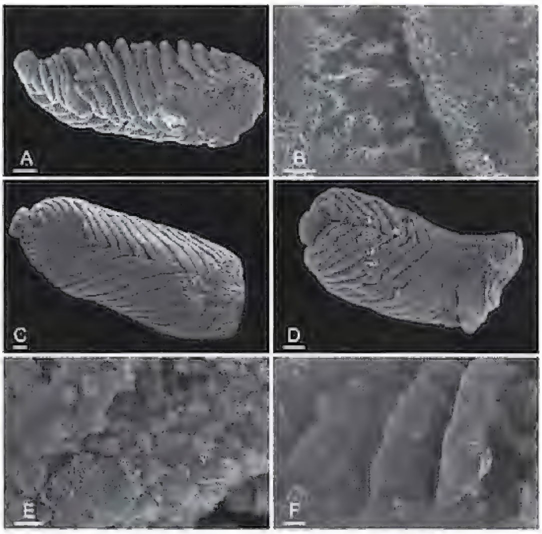

FIGURE 89. *Tayuva lilacina* (Indo-West Pacific), rhinophores and gills. A. Rhinophore, CASIZ 065363, scale = 100 µm.— B. Rhinophoral lamellae, CASIZ 065363, scale = 10 µm.— C. Rhinophore, CASIZ 073468, scale = 100 µm.— D. Rhinophore, CASIZ 068753 (#1), scale = 100 µm.— E. Branchial plume, detail, 068753 (#1), scale = 30 µm.— F. Branchial plume, detail, AM C132958 (#3), scale = 10 µm.

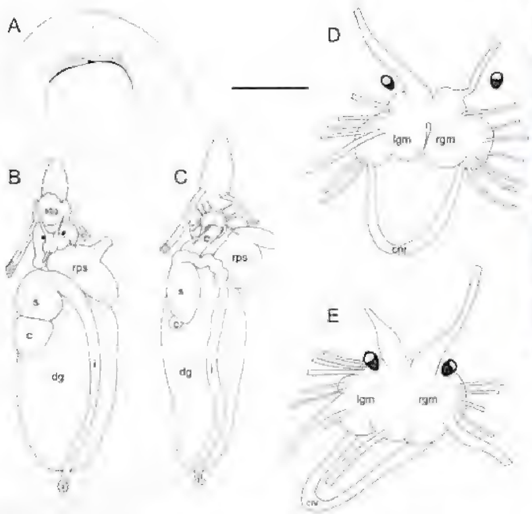

FIGURE 90. *Tayuva lilacina* (Indo-West Pacific). A. Anterior, ventral view, MV F86423, scale = 6 mm.— B. General anatomy, MV F86423, scale = 2.6 mm.— C. General anatomy, scale = 6 mm.— D. Nervous system, CASIZ 156947, scale = 0.6 mm.— E. Nervous system, MV F86423, scale = 0.7 mm.

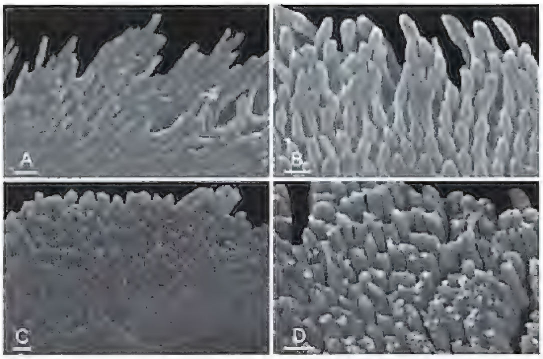

FIGURE 91. *Tayuva lilacina* (Indo-West Pacific), jaws, Hawaii and Marshall Islands. A. CASIZ 031862, scale = 10 µm.— B. CASIZ 086958, scale = 10 µm.— C. CASIZ 168913, scale = 10 µm.— D. CASIZ 121234, scale = 10 µm.

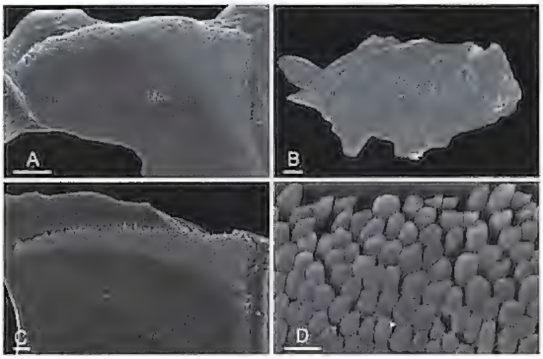

FIGURE 92. *Tayuva lilacina* (Indo-West Pacific), jaws, Indonesia and Japan. A. CASIZ 158266, scale = 100 µm.— B. CAISZ 068283, scale = 100 µm.— C. CASIZ 103770, scale = 30 µm.— D. CASIZ 103770, scale = 10 µm.

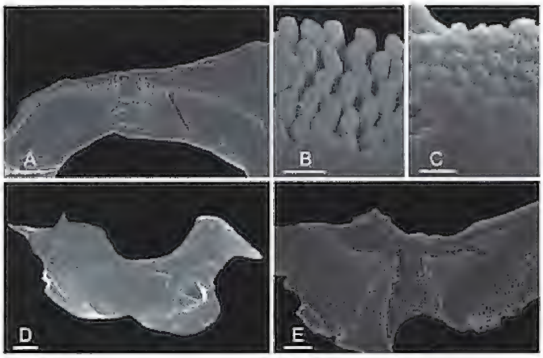

FIGURE 93. *Tayuva lilacina* (Indo-West Pacific), jaws, Papua New Guinea. A. CASIZ 072829, scale = 100 µm.— B. CASIZ 062829, scale = 10 µm.— C. CASIZ 065365, scale = 10 µm.— D. CASIZ 065363, scale = 200 µm.— E. CASIZ 071610, scale = 30 µm.

prostatic parts were hardly distinguishable because the prostate was homogeneously whitish or because the reproductive system was not fully mature. The deferent duct is short. It is straight or loosely convoluted. Distinct loops are seldom observed (CASIZ 068753 #1). The proximal part of the deferent duct that just follows the prostate is wide and folded longitudinally; the folds are internal but clearly distinct externally. Exceptionally, this folded proximal part of the deferent duct can also be narrow (NMV F86423, CASIZ 068283) or absent (CASIZ 099332, AM C132978 #2, CASIZ 068753 #1, CASIZ 071610, CASIZ 072829, CASIZ 031862, CASIZ 061455 #2). The deferent duct ends in a distinct penis (i.e., which does not correspond to the evaginable distal part of the deferent duct). The penis is unarmed. It is cylindrical with a narrower apex (apical tail); the latter, sometimes, is slightly coiled. The relative length of the base and the apex vary among individuals. A large and short base is usually associated with a long apex, whereas a narrow and long base is associated with a short apex. Some cilia may be observed on the surface of the penis, if well preserved.

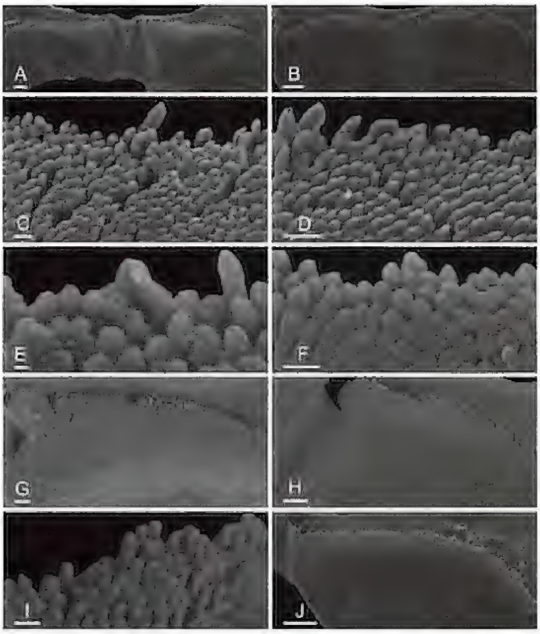

FIGURE 94. *Tayuva lilacina* (Indo-West Pacific), jaws, New South Wales. A. AM C115270 (#1), scale = 100 µm.— B. AM C123599, scale = 200 µm.— C. AM C115270 (#1), scale = 10 µm.— D. AM C123599, scale = 20 µm.— E. AM C125186, scale = 3 µm.— F. AM C132958 (#5), scale = 10 µm.— G. AM C142251 (#1), scale = 30µm.— H. MV F86423, scale = 40 µm.— I. MV F86422, scale = 10 µm.— J. AM C132317, scale = 100 µm.

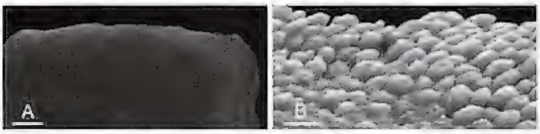

FIGURE 95. *Tayuva lilacina* (Indo-West Pacific), jaws, CASIZ 073468. A. Scale = 100 µm.— B. Scale = 10 µm.

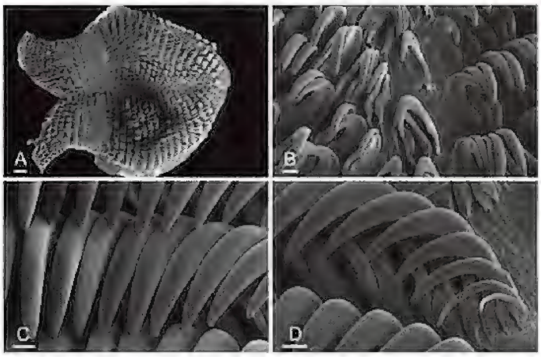

FIGURE 96. *Tayuva lilacina* (Indo-West Pacific), radula, CASIZ 031862, Hawaii. A. Scale = 200 µm.— B. Innermost teeth, scale = 20 µm.— C. Median teeth, scale = 20 µm.— D. Outermost teeth, scale = 20 µm.

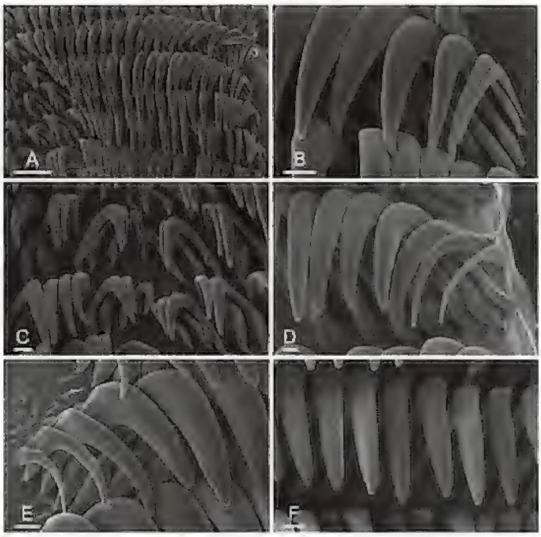

FIGURE 97. *Tayuva lilacina* (Indo-West Pacific), radula, Hawaii. A. Right rows, CASIZ 061455 (#2), scale = 100 µm.— B. Outermost teeth, CASIZ 061455 (#2), scale = 20 µm.— C. Innermost teeth, CASIZ 061455 (#2), scale = 20 µm.— D. Outermost teeth, CASIZ 071572, scale = 10 µm.— E. Outermost teeth, CASIZ 086958, scale = 20 µm.— F. Median teeth, CASIZ 086958, scale = 20 µm.

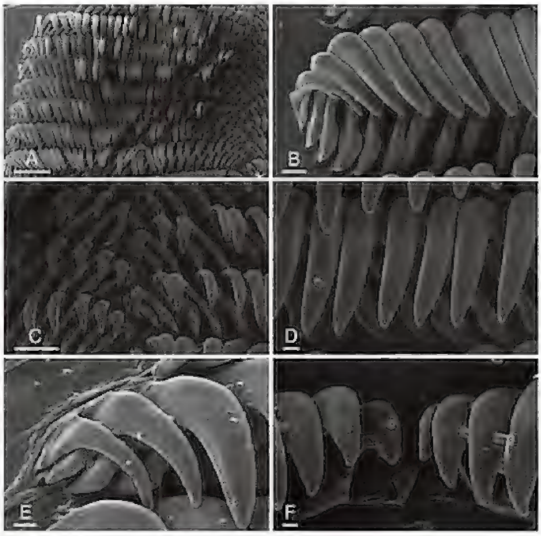

FIGURE 98. *Tayuva lilacina* (Indo-West Pacific), radula, Marshall Islands. A. Right rows, CASIZ 168913, scale = 200 µm.— B. Outermost teeth, CASIZ 168913, scale = 30 µm.— C. Innermost teeth, CASIZ 168913, scale = 100 µm.— D. Median teeth, CASIZ 168913, scale = 20 µm.— E. Outermost teeth, CASIZ 121234, scale = 20 µm.— F. Innermost teeth, CASIZ 121234, scale = 10 µm.

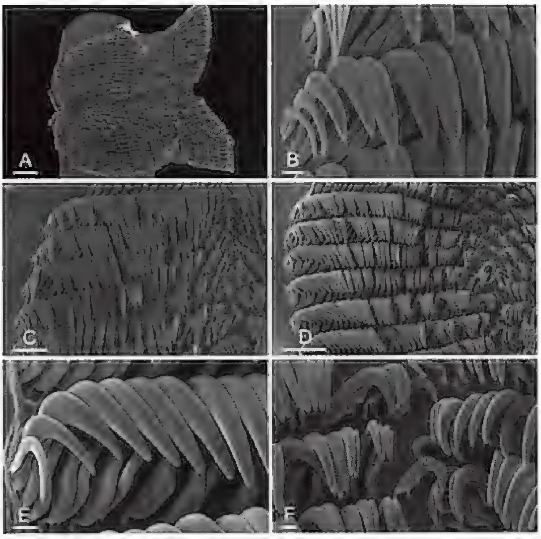

FIGURE 99. *Tayuva lilacina* (Indo-West Pacific), radula, Philippines. A. CASIZ 133770, scale = 200 µm.— B. Outermost teeth, CASIZ 133770, scale = 20 µm.— C. Left rows, CASIZ 133770, scale = 100 µm.— D. Left rows, CASIZ 158266, scale = 200 µm.— E. Outermost teeth, CASIZ 158266, scale = 20 µm.— F. Innermost teeth, CASIZ 158266, scale = 20 µm.

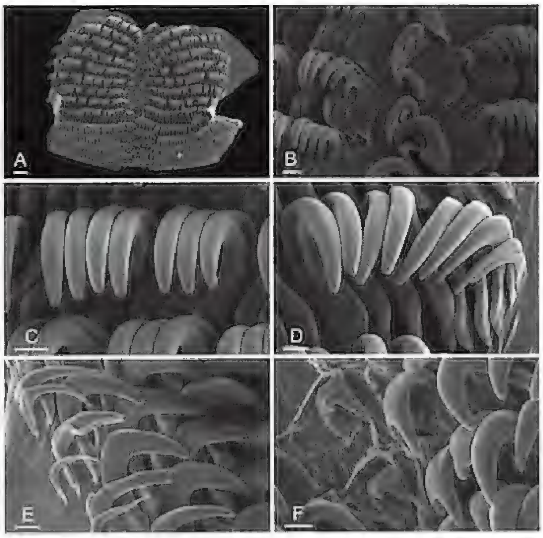

FIGURE 100. *Tayuva lilacina* (Indo-West Pacific), radula, Philippines and Indonesia. A. CASIZ 068283, scale = 100 µm.— B. Innermost teeth, CASIZ 068283, scale = 20 µm.— C. Median teeth, CASIZ 068283, scale = 20 µm.— D. Outermost teeth, CASIZ 068283, scale = 20 µm.— E. Outermost teeth, CASIZ 156947, scale = 20 µm.— F. Innermost teeth, CASIZ 156947, scale = 20 µm.

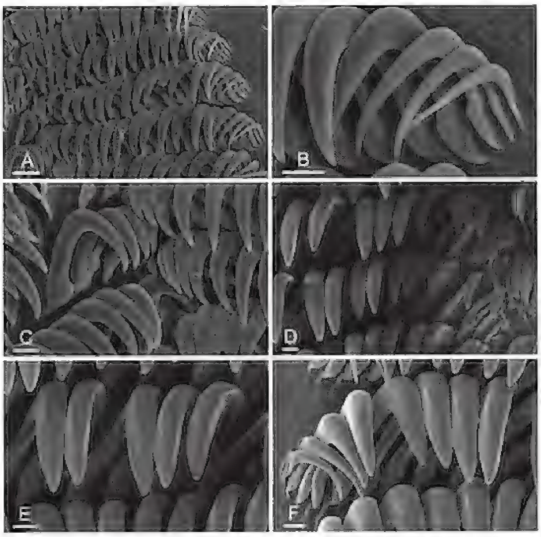

FIGURE 101. *Tayuva lilacina* (Indo-West Pacific), radula, Papua New Guinea. A. Right rows, CASIZ 065365, scale = 40 µm.— B. Outermost teeth, CASIZ 065365, scale = 20 µm.— C. Innermost teeth, CASIZ 065365, scale = 20 µm.— D. Innermost teeth, CASIZ 065363, scale = 20 µm.— E. Median teeth, CASIZ 065363, scale = 20 µm.— F. Outermost teeth, CASIZ 065363, scale = 20 µm.

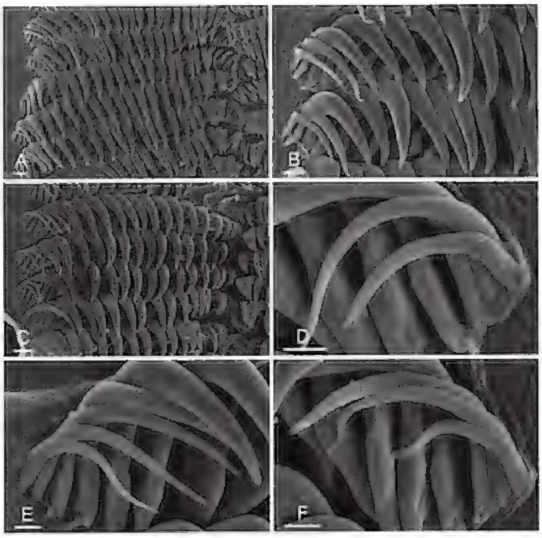

FIGURE 102. *Tayuva lilacina* (Indo-West Pacific), radula, Papua New Guinea. A. Left rows, CASIZ 072829, scale = 30 µm.— B. Outermost teeth, CASIZ 072829, scale = 20 µm.— C. Left rows, CASIZ 071610, scale = 30 µm.— D. Outermost teeth, CASIZ 071610, scale = 10 µm.— E. Outermost teeth, CASIZ 071610, scale = 10 µm.— F. Outermost teeth, CASIZ 071610, scale = 10 µm.

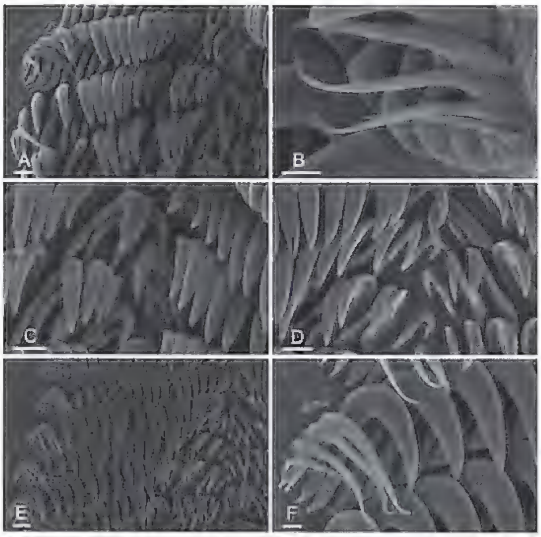

FIGURE 103. *Tayuva lilacina* (Indo-West Pacific), radula, Papua New Guinea. A. Left rows, CASIZ 072830, scale = 20 µm.— B. Outermost teeth, CASIZ 072830, scale = 10 µm.— C. Innermost teeth, CASIZ 072830, scale = 20 µm.— D. Innermost teeth, CASIZ 086307 (#1), scale = 20 µm.— E. Left rows, CASIZ 086307 (#1), scale = 20 µm.— F. Outermost teeth, CASIZ 086307 (#1), scale = 10 µm.

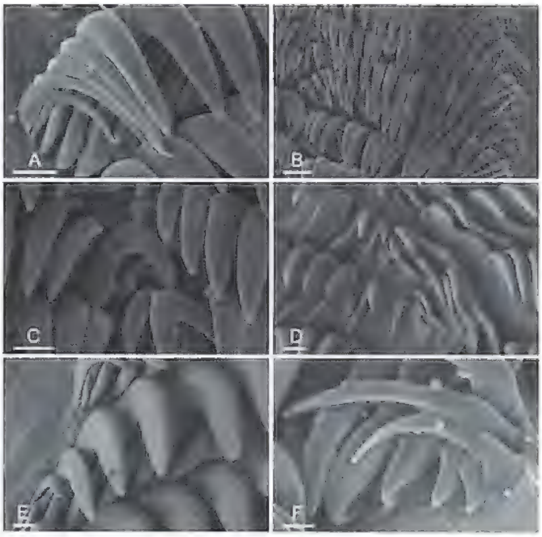

FIGURE 104. *Tayuva lilacina* (Indo-West Pacific), radula, New South Wales. A. Outermost teeth, AM C132958 (#5), scale = 20 µm.— B. Right rows, AM C132958 (#5), scale = 40 µm.— C. Innermost teeth, AM C132958 (#5), scale = 20 µm.— D. Innermost teeth, MV F86423, scale = 30 µm.— E. Outermost teeth, MV F86423, scale = 20 µm.— F. Outermost teeth, AM C132958 (#1), scale = 10 µm.

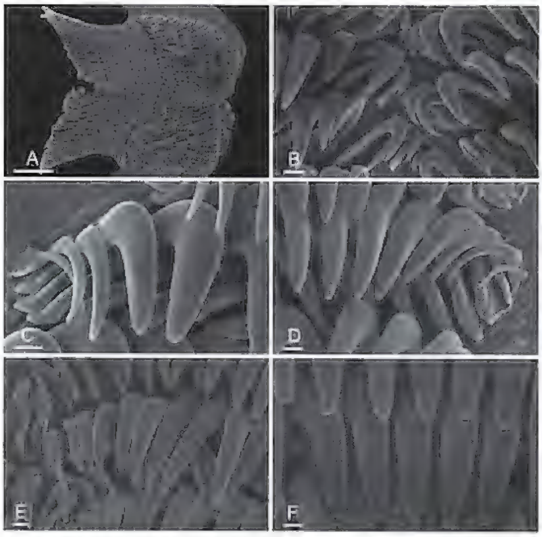

FIGURE 105. *Tayuva lilacina* (Indo-West Pacific), radula, New South Wales. A. AM C125186, scale = 300 µm.— B. Innermost teeth, AM C125186, scale = 20 µm.— C. Outermost teeth, AM C125186, scale = 20 µm.— D. Outermost teeth, AM C115270 (#1), scale = 20 µm.— E. Innermost teeth, AM C115270 (#1), scale = 20 µm.— F. Median teeth, AM C115270 (#1), scale = 20 µm.

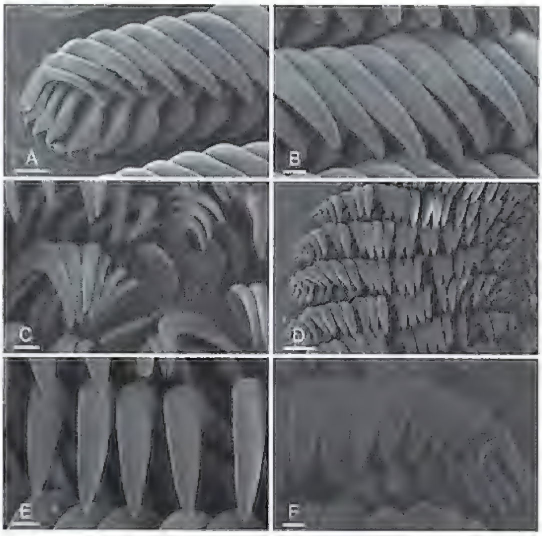

FIGURE 106. *Tayuva lilacina* (Indo-West Pacific), radula, New South Wales. A. Outermost teeth, MV F86422, scale = 30 µm.— B. Median teeth, MV F86422, scale = 20 µm.— C. Innermost teeth, MV F86422, scale = 20 µm.— D. Left rows, AM C142251 (#1), scale = 100 µm.— E. Median teeth, AM C142251 (#1), scale = 20 µm.— F. Outermost teeth, AM C142251 (#1), scale = 20 µm.

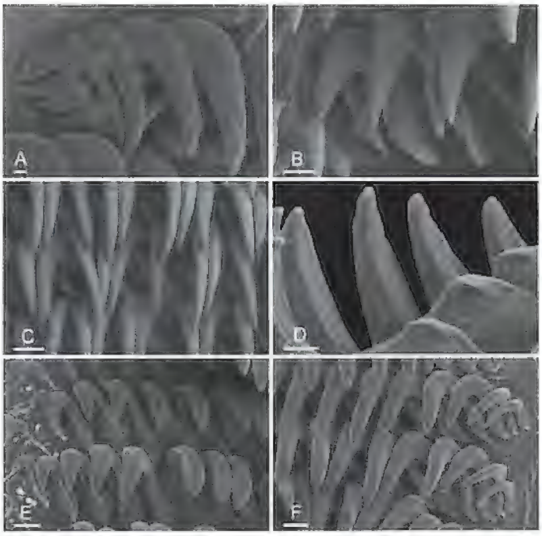

FIGURE 107. *Tayuva lilacina* (Indo-West Pacific), radula, New South Wales. A. Outermost teeth, AM C418420, scale = 10 µm.— B. Innermost teeth, AM C418420, scale = 20 µm.— C. Median teeth, AM C418420, scale = 40 µm.— D. Inferior side of the hook of median teeth, AM C418420, scale = 20 µm.— E. Innermost teeth, AM C123599, scale = 40 µm.— F. Outermost teeth, AM C123599, scale = 40 µm.

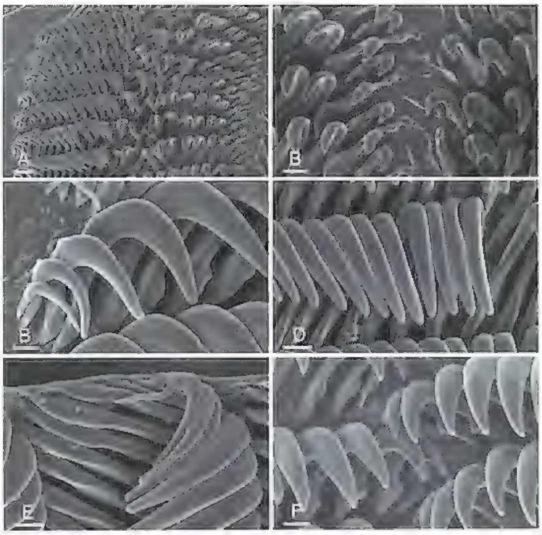

FIGURE 108. *Tayuva lilacina* (Indo-West Pacific), radula, Madagascar, South Africa, Tanzania. A. Left rows, CASIZ 073468, scale = 100 µm.— B. Innermost teeth, CASIZ 073468, scale = 40 µm.— C. Outermost teeth, CASIZ 073468, scale = 20 µm.— D. Median teeth, CASIZ 099332, scale = 30 µm.— E. Outermost teeth, CASIZ 099332, scale = 20 µm.— F. Innermost teeth, CASIZ 073241, scale = 20 µm.

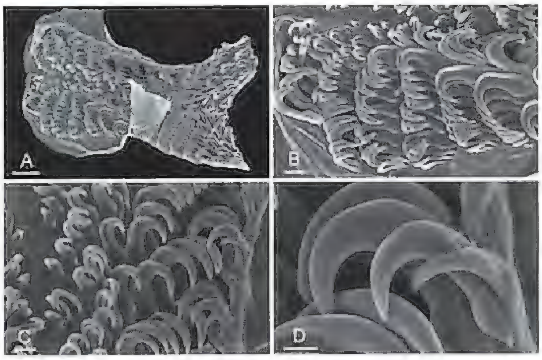

FIGURE 109. *Tayuva lilacina* (Indo-West Pacific), uncertain, CASIZ 073266. A. Scale = 100 µm.— B. Left rows, scale = 30 µm.— C. Right rows, scale = 20 µm.— D. Outermost teeth, scale = 10 µm.

The maximum, total length of the penis is 2 mm (CASIZ 061455 #2). However, the majority of the specimens have a penis that is less than 1 mm long. All the specimens dissected here have a penis that is easy to recognize, acknowledging some variation mentioned above. A penis was absent in two immature specimens though (AM C132958 #5 and #6); and two specimens whose identification is uncertain (CASIZ 073266, CASIZ 078454). The vaginal duct is straight or loosely convoluted. The deferent duct and the vaginal duct join together and form a vestibule that may or may not remain separate from the female duct. A muscular wall protects the distal part of the reproductive system. It usually protects the penial sheath but may be broader and surround the vestibule formed by the deferent duct and the vaginal duct. More exceptionally, it may surround the female genital duct as well. The muscular wall may be present but not conspicuous (AM C132958 #5, CASIZ 072830, CASIZ 157146) or clearly absent (CASIZ 099332, AM C132978 #1, CASIZ 068283, CASIZ 068753 #1, CASIZ 071610, CASIZ 072829, CASIZ 031862, CASIZ 061455, CASIZ 071572). This variation is probably caused by a combination of several effects, including maturity as well as natural variation among adult, fully mature individuals. Note that all the specimens that lack a muscular wall have a distinct *lilacina*-like penis. The fertilization duct is short. Typically, it makes a single loose loop near the bursa copulatrix. Exceptionally, this loop is

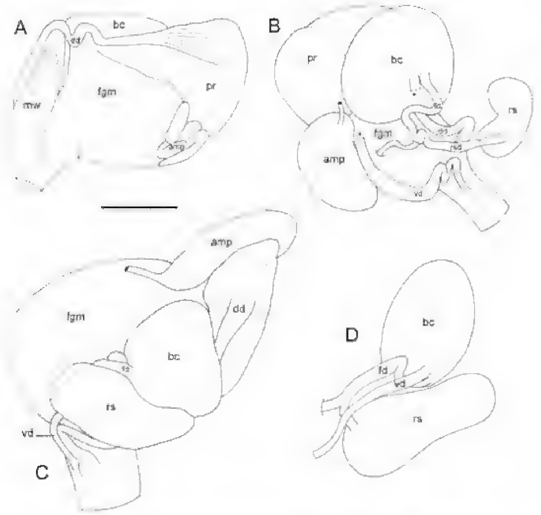

FIGURE 110. *Tayuva lilacina* (Indo-West Pacific), reproductive system, Hawaii. A. CASIZ 086958, scale = 1.3 mm.— B. CASIZ 061455 (#2), scale = 1.5 mm.— C. CASIZ 071572, scale = 2 mm.— D. CASIZ 071572, scale = 2 mm.

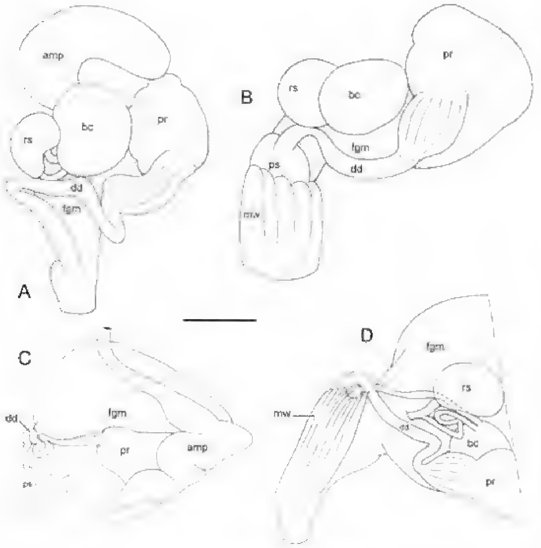

FIGURE 112. *Tayuva lilacina* (Indo-West Pacific), reproductive system, Japan, Indonesia, Papua New Guinea. A. CASIZ 072829, scale = 0.6 mm.— B. CASIZ 072830, scale = 1.1 mm.— C. CASIZ 068283, scale = 1.1 mm.— D. CASIZ 069969 (prostate and female gland mass cut), scale = 1.1 mm.

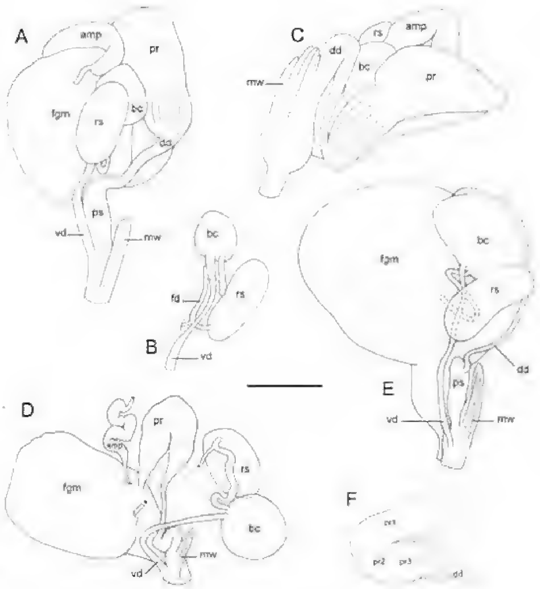

FIGURE 111. *Tayuva lilacina* (Indo-West Pacific), reproductive system, Philippines and Marshall Islands. A. CASIZ 103770, scale = 1.7 mm.— B. CASIZ 103770, scale = 1.5 mm.— C. CASIZ 156947, scale = 1.6 mm.— D. CASIZ 168914, scale = 2.5 mm.— E. CASIZ 168913, scale = 2 mm.— F. CASIZ 168913, scale = 1.7 mm.

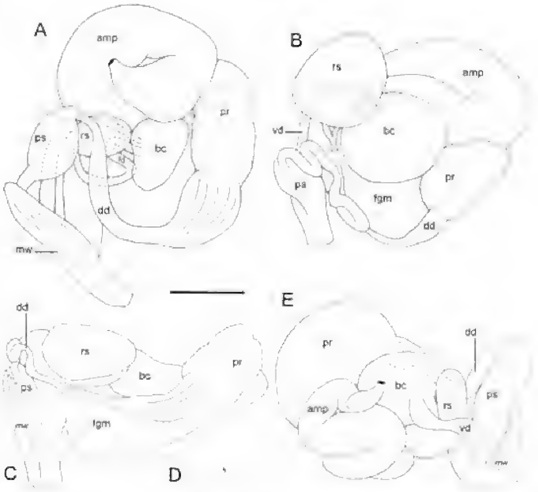

FIGURE 113. *Tayuva lilacina* (Indo-West Pacific), reproductive system, Papua New Guinea. A. CASIZ 068753 (#2), scale = 0.5 mm.— B. CASIZ 068753 (#1), scale = 0.5 mm.— C. CASIZ 065363, scale = 1 mm.— D. CASIZ 065363, scale = 1 mm.— E. CASIZ 086307 (#1), scale = 0.6 mm.

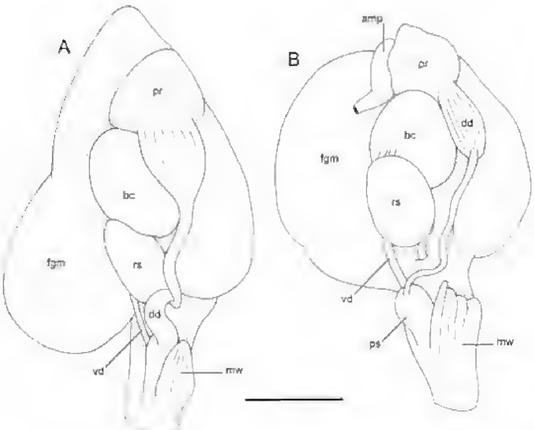

FIGURE 114. *Tayuva lilacina* (Indo-West Pacific), reproductive system, Lord Howe Island. A. AM C132317, scale = 1 mm.— B. AM C418420, scale = 1.2 mm.

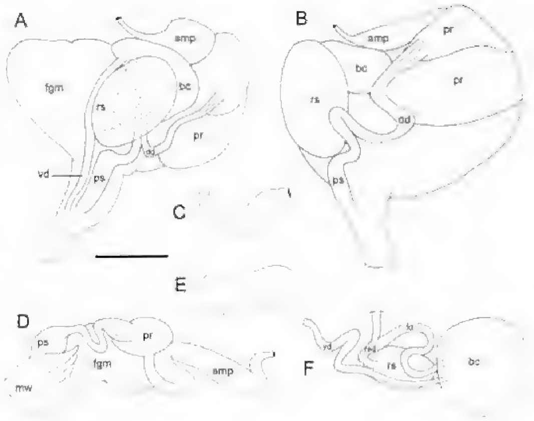

FIGURE 115. *Tayuva lilacina* (Indo-West Pacific), reproductive system, New South Wales. A. MV F86423, scale = 1.3 mm.— B. MV F86423, scale = 1 mm.— C. Penis, MV F86423, scale = 0.8 mm.— D. AM C 125186, scale = 0.6 mm.— E. Penis, AM C 125186, scale = 0.3 mm.— F. AM C 125186, scale = 0.4 mm.

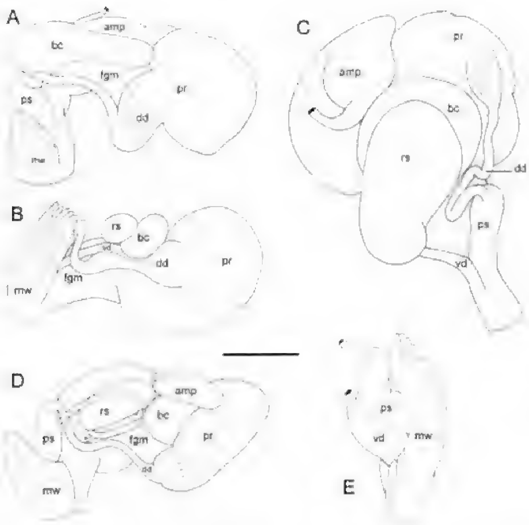

FIGURE 116. *Tayuva lilacina* (Indo-West Pacific), reproductive system, New South Wales. A. MV F86422, scale = 1.3 mm.— B. AM C132958 (#1), scale = 0.8 mm.— C. AM C132978, scale = 0.6 mm.— D. AM C 123599, scale = 1.2 mm.— E. AM C155707, scale = 1 mm.

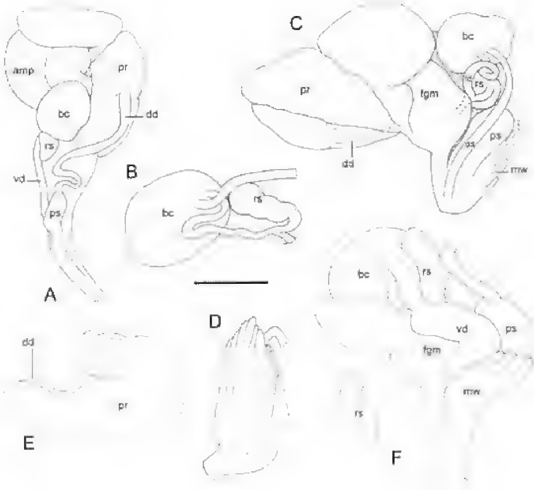

FIGURE 117. *Tayuva lilacina* (Indo-West Pacific), reproductive system, Tanzania, Madagascar, South Africa. A. CASIZ 099332, scale = 2.2 mm.— B. Spermatic pouches, CASIZ 099332, scale = 0.6 mm.— C. CASIZ 073241, scale = 0.8 mm.— D. Muscular wall, CASIZ 073231, scale = 0.5 mm.— E. Prostate and proximal deferent duct, CASIZ 073468, scale = 1.5 mm.— F. CASIZ 073468, scale = 1.2 mm.

longer and form two or three tight loops (AM C115270 #1, CASIZ 072829). The connection between the fertilization duct and the female gland mass is marked by a short, distinct duct. The duct of the receptaculum seminis is short and distinct too. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is hidden behind the receptaculum seminis. The relative size of the receptaculum seminis and the bursa copulatrix

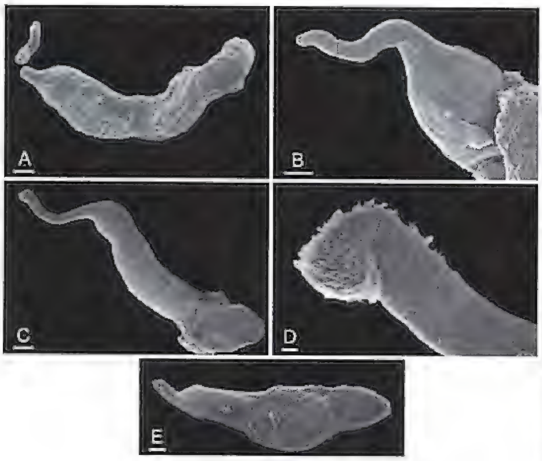

FIGURE 118. *Tayuva lilacina* (Indo-West Pacific), penis, Hawaii. A. CASIZ 061455 (#2), scale = 100 μm.— B. CASIZ 086958, scale = 100 μm.— C. CASIZ 031862, scale = 100 μm.— D. CASIZ 031862, scale = 10 μm.— E. CASIZ 071572, scale = 100 μm.

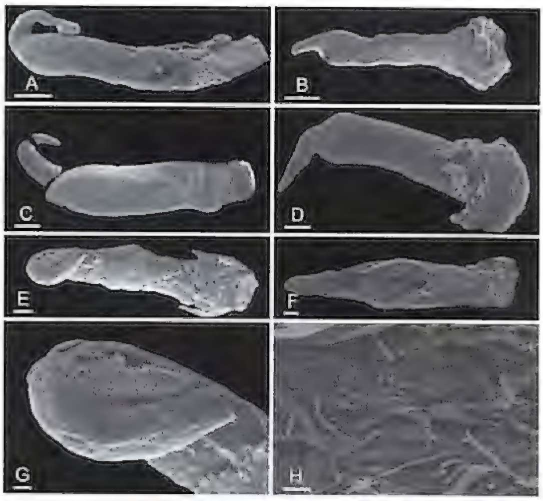

FIGURE 119. *Tayuva lilacina* (Indo-West Pacific), penis, Indonesia and Japan. A. CASIZ 068283, scale = 100 μm.— B. CASIZ 068283, scale = 100 μm.— C. CASIZ 156947, scale = 100 μm.— D. CASIZ 133770, scale = 100 μm.— E. CASIZ 069969, scale = 100 μm.— F. Distal muscular wall, CASIZ 133770, scale = 100 μm.— G. CASIZ 069969, scale = 30 μm.— H. Distal muscular wall, detail, CASIZ 133770, scale = 20 μm.

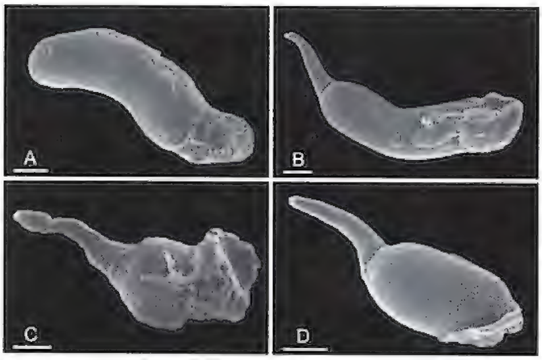

FIGURE 120. *Tayuva lilacina* (Indo-West Pacific), penis, Papua New Guinea. A. Penis (narrow apex lost during preparation), CASIZ 086307 (#1), scale = 100 μm.— B. CASIZ 065365, scale = 100 μm.— C. CASIZ 072830, scale = 100 μm.— D. CASIZ 068753 (#2), scale = 100 μm.

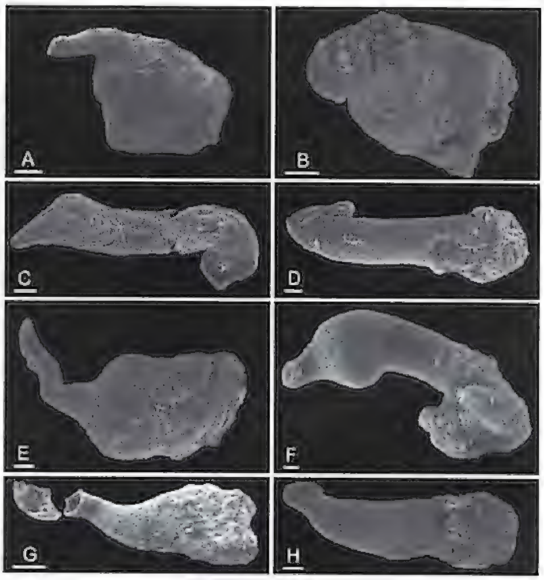

FIGURE 121. *Tayuva lilacina* (Indo-West Pacific), penis, New South Wales. A. AM C142251 (#1), scale = 100 μm.— B. AM C142251 (#2), scale = 100 μm.— C. AM C132317, scale = 100 μm.— D. AM C113759, scale = 100 μm.— E. AM C123599, scale = 100 μm.— F. AM C155707 (#2), scale = 100 μm.— G. AM C132958 (#1), scale = 60 μm.— H. AM C418422, scale = 100 μm.

varies from 2/1 to 1/4. In most specimens, the bursa copulatrix is slightly larger than the receptaculum seminis. Exceptionally, the size of the bursa copulatrix equals six (AM C126481) or ten (AM C142251 #1) times the size of the receptaculum seminis. The bursa copulatrix is spherical-ovate. The receptaculum can be spherical-ovate (e.g., AM C125186, AM C418422, AM C132958 #1, CASIZ 168913) or sausage-shaped (e.g., AM C126481, AM

C132958 #2). However, in most specimens, the shape of the receptaculum seminis is in between spherical-ovate and sausage-shaped. Finally, the surface of the receptaculum seminis is smooth and shiny. No reproductive system was found in three specimens below 12 mm preserved length, certainly because of their small size (CASIZ 078454, CASIZ 073266, AM C132958 #6). However, it is worth pointing out that a reproductive system was found in other small specimens within the same range of sizes, below 12 mm preserved length (e.g., AM C132958 #5, CASIZ 068753 #1 and #2, CASIZ 071610, CASIZ 072830), although one of these was immature and had no penis yet (AM C132958 #5).

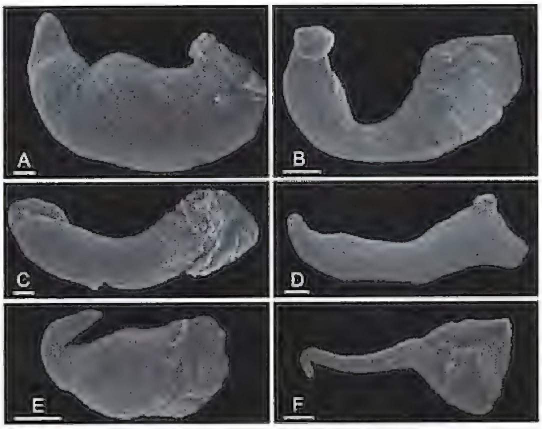

FIGURE 122. *Tayuva lilacina* (Indo-West Pacific), penis, NSW. A. AM C132978 (#2), scale = 20 µm.— B. MV F86423, scale = 100 µm.— C. AM C126481, scale = 100 µm.— D. AM C132978 (#1), scale = 40 µm.— E. AM C132958 (#2), scale = 100 µm.— F. AM C418420, scale = 100 µm.

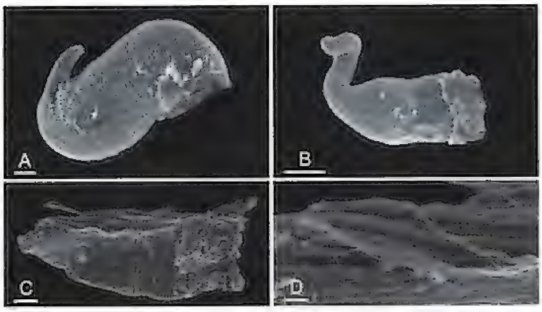

FIGURE 123. *Tayuva lilacina* (Indo-West Pacific), penis Madagascar, South Africa, Tanzania. A. CASIZ 073468, scale = 100 µm.— B. CASIZ 099332, scale = 100 µm.— C. Distal muscular wall, CASIZ 073241, scale = 100 µm.— D. Distal muscular wall, detail, CASIZ 073241, scale = 20 µm.

DESCRIPTION OF A FEW PROBLEMATIC SPECIMENS (CASIZ 069742, CASIZ 083651, CASIZ 086307 #2 and #3, CASIZ 083744, CASIZ 083820, CASIZ 096341, Figs. 124-133).— In order not to repeat the full description provided above, only the differences are emphasized. Unfortunately, no pictures of live animals were available for these specimens. However, Terry Gosliner, who collected them, identified them as *Discodoris fragilis* (i.e., *lilacina*), which indicates that these specimens did not strikingly differ externally from the specimens described above. No noticeable differences could be detected in the preserved color, the external morphology, the digestive system (including the radula), and the nervous system. However, these specimens are problematic because their penis differs from that of the specimens described above, although the general organization of their reproductive system was globally similar. One fully mature specimen from the Philippines (CASIZ 083744) does not have a distal muscular wall, a folded proximal part of the deferent duct, nor a penis. One fully mature specimen from the Philippines (CASIZ 096341) has a wide folded proximal part of the deferent duct, no muscular wall, and a cylindrical penis with no distinct apical tail. One fully mature specimen from the Philippines (CASIZ 083820,) has a wide folded proximal part of the deferent duct, no muscular wall, and a conical penis with no distinct apical tail. One specimen from the Philippines (CASIZ 083651) has an immature reproductive system with a wide folded proximal part of the deferent duct, a small muscular wall, and a tiny, conical penis, with no distinct apical tail. One specimen from Papua New Guinea (CASIZ 086307 #2) has a highly convoluted deferent duct (with five loops), a wide folded proximal part of the deferent duct, no muscular wall, and a cylindrical penis, with no distinct apical tail, and with large conical humps irregularly placed on the second half of its length. Another specimen from the same locality (CASIZ 086307 #3) has no wide folded proximal part of the deferent duct, no muscular wall, and a peculiar apical tail (though close to

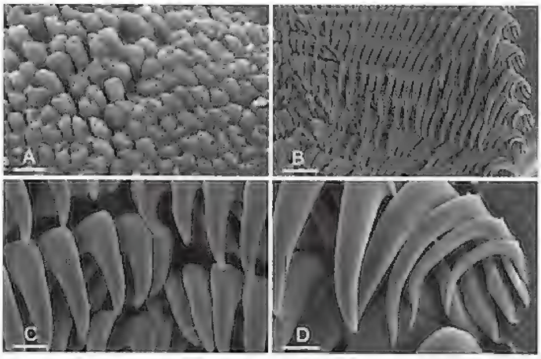

FIGURE 124. *Tayuva lilacina* (Indo-West Pacific), problematic CASIZ 069742 (#1). A. Jaw rodlets, scale = 10 µm.— B. Right rows, scale = 100 µm.— C. Innermost teeth, scale = 20 µm.— D. Outermost teeth, scale = 20 µm.

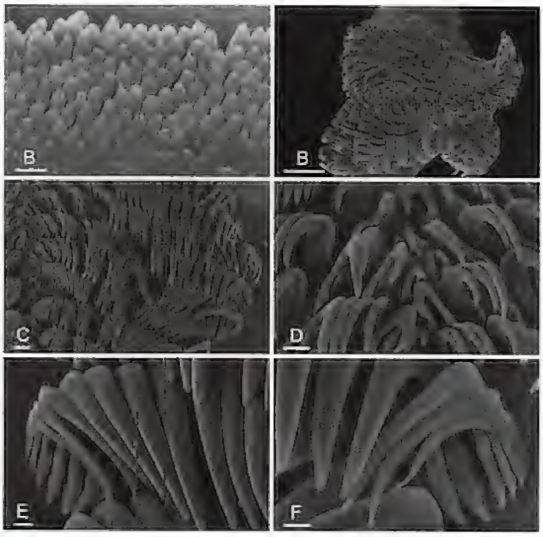

FIGURE 125. *Tayuva lilacina* (Indo-West Pacific), problematic CASIZ 069742 (#3). A. Jaw rodlets, scale = 10 µm.— B. Radula, scale = 200 µm.— C. Right rows, scale = 30 µm.— D. Innermost teeth, scale = 20 µm.— E. Outermost teeth, scale = 10 µm.— F. Outermost teeth, scale = 10 µm.

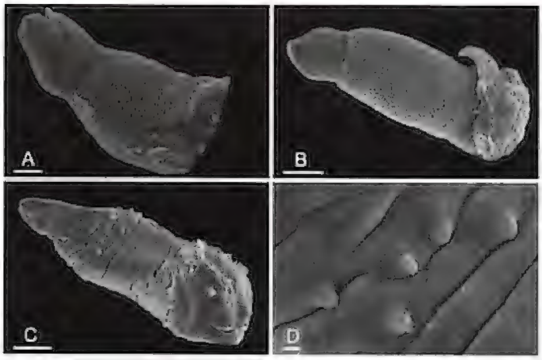

FIGURE 126. *Tayuva lilacina* (Indo-West Pacific), problematic CASIZ 069742, penis. A. CASIZ 069742 (#1), scale = 40 µm.— B. CASIZ 069742 (#2), scale = 100 µm.— C. CASIZ 069742 (#3), scale = 100 µm.— D. CASIZ 069742 (#3), scale = 10 µm.

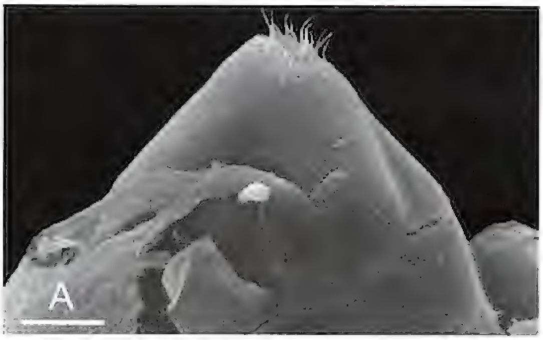

FIGURE 127. *Tayuva lilacina* (Indo-West Pacific), problematic CASIZ 083651, penis. A. Scale = 20 µm.

that of a 'typical' specimen from New South Wales – AM C155707 #2). One specimen from Papua New Guinea (CASIZ 069742 #1) has a wide folded proximal part of the deferent duct, a small muscular wall, a quite convoluted (a few tight loops) deferent duct, and a cylindrical penis, with no apical tail, and divided in two parts. Another specimen from the same locality (CASIZ 069742 #2) has a similar reproductive system, except that it has no muscular wall. A third specimen from the same locality (CASIZ 069742 #3) has a fertilization duct with three tight loops instead of one near the bursa copulatrix, a deferent duct more or less straight with a narrow folded proximal part, no distal muscular wall, a cylindrical penis with a large conical apex, with small, conical, soft papillae between the cylindrical base of the penis and the conical apex.

INFRA-SPECIFIC CHARACTER VARIATION (INDO-WEST PACIFIC REGION).— The problematic specimens are not included here (see discussion). The information available in the literature is largely congruent with the description provided here. The largest live animals are: an individual from the Marshall Islands (CASIZ 168913), with a 50 mm preserved length, which should correspond to a 75 mm maximum length, alive, and a individual from Hawaii (CASIZ 061455 #1), with a 58 mm preserved length. Maximum lengths in the literature are: 35 mm, alive, for specimens

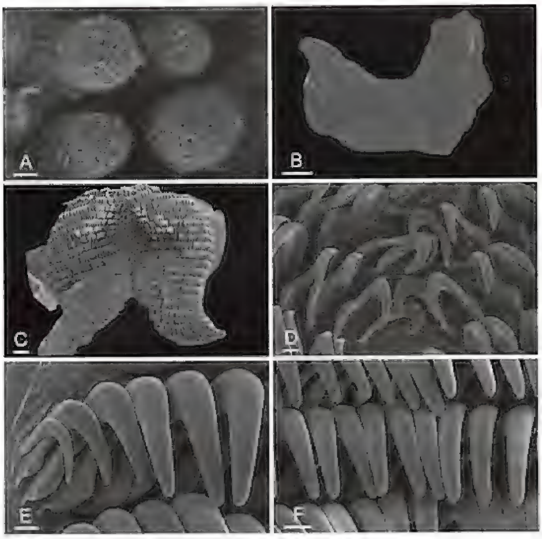

FIGURE 128. *Tayuva lilacina* (Indo-West Pacific), problematic CASIZ 083744. A. Dorsal notum, scale = 40 µm.— B. Smooth labial cuticle, scale = 400 µm.— C. Radula, scale = 200 µm.— D. Innermost teeth, scale = 20 µm.— E. Outermost teeth, scale = 20 µm.— F. Median teeth, scale = 40 µm.

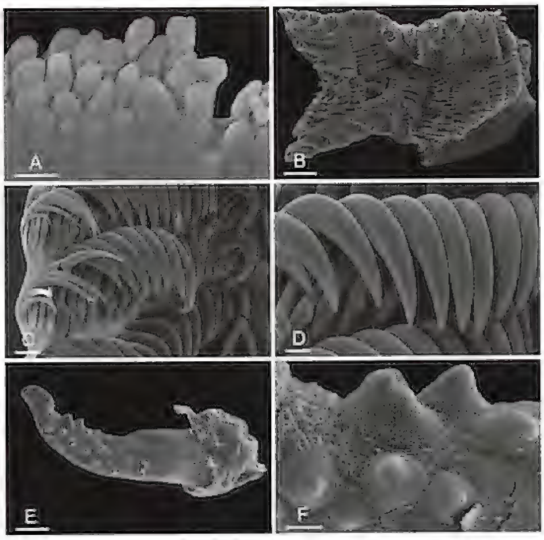

FIGURE 129. *Tayuva lilacina* (Indo-West Pacific), problematic CASIZ 086307 (#2). A. Jaw rodlets, scale = 10 µm.— B. Radula, scale = 100 µm.— C. Left rows, scale = 20 µm.— D. Median teeth, scale = 10 µm.— E. Penis, scale = 100 µm.— F. Penis, detail, scale = 20 µm.

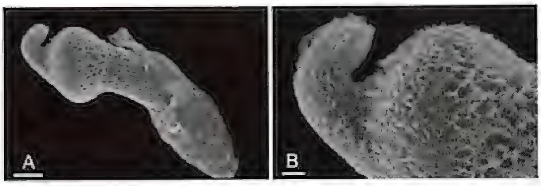

FIGURE 130. *Tayuva lilacina* (Indo-West Pacific), problematic CASIZ 086307 (#3). A. Penis, scale = 40 µm.— B. Penis, apex, scale = 10 µm.

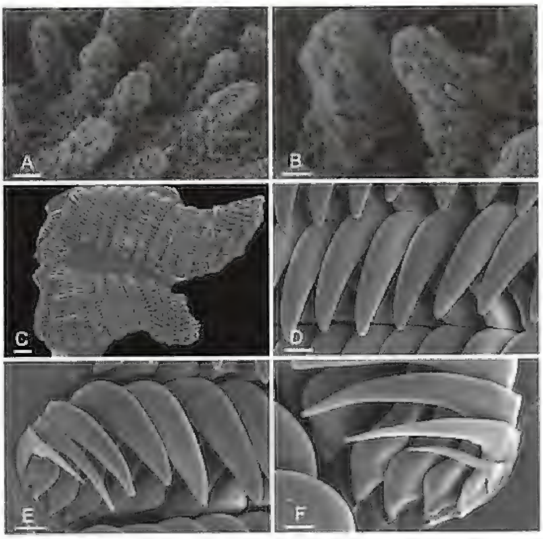

FIGURE 131. *Tayuva lilacina* (Indo-West Pacific), problematic CASIZ 096341. A. Dorsal notum, scale = 40 µm.— B. Dorsal notum, scale = 20 µm.— C. Radula, scale = 100 µm.— D. Median teeth, scale = 20 µm.— E. Outermost teeth, scale = 20 µm.— F. Outermost teeth, scale = 10 µm.

from Hawaii (Kay and Young 1969, as *fragilis*); 35 mm, alive, for specimens from southern Japan (Suzuki 2000, as *lilacina*); 52 mm, alive, for specimens from Australia (Allan 1933, 1947, 1950, as *palma*; Marshall and Willan 1999, as *palma*). In average, specimens dissected in the present study from Australia, Hawaii, Marshall Islands, Japan, South Africa and Tanzania tend to be larger than the specimens from Madagascar, Papua New Guinea, the Philippines, and Indonesia. Also, the specimens from southern New South Wales tend to be larger than the specimens from northern New South Wales. Based on data available both in the present study and in the literature, the variation of the color of the dorsal notum does not seem to be correlated with any particular geographical distribution. This, however, does not mean that no correlation could be found in the future between color and distribution. The radular formulae found in the literature are compatible with the formulae provided here: 20 × (28-0-28) in a 23 mm long

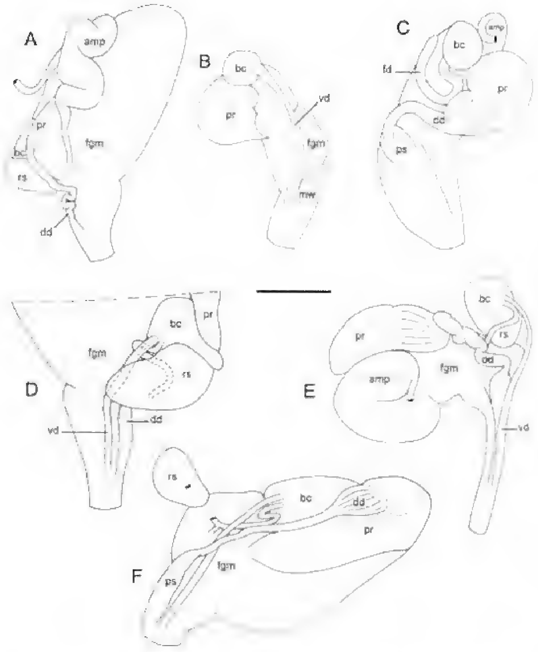

FIGURE 132. *Tayuva lilacina* (Indo-West Pacific), problematic, reproductive system. A. CASIZ 083744, scale = 2 mm.— B. CASIZ 083651, scale = 0.8 mm.— C. CASIZ 083651, scale = 0.6 mm.— D. CASIZ 083744, scale = 1 mm.— E. CASIZ 096341, scale = 1 mm.— F. CASIZ 083820, scale = 1 mm.

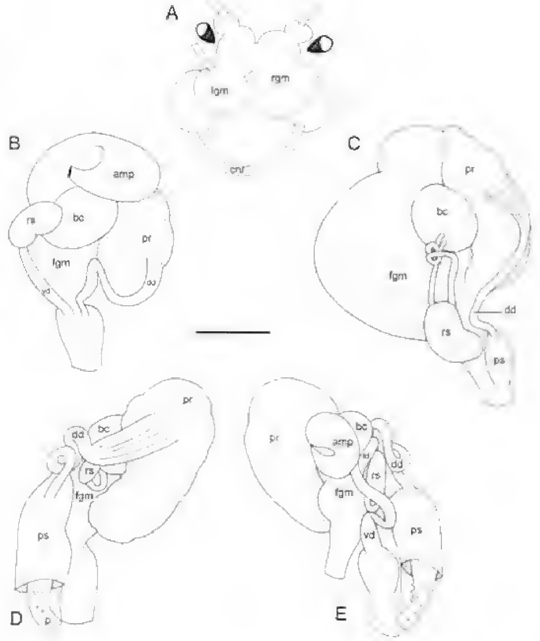

FIGURE 133. *Tayuva lilacina* (Indo-West Pacific), problematic, nervous and reproductive systems. A. Nervous system, CASIZ 086307 (#2), scale = 0.3 mm.— B. CASIZ 086307 (#3), scale = 0.4 mm.— C. CASIZ 069742 (#3), scale = 1 mm.— D. CASIZ 086307 (#2), scale = 0.5 mm.— E. CASIZ 086307 (#2), scale = 0.5 mm.

preserved specimen (Marcus and Marcus 1970c), and 18/22 × (28/30-0-28/30) in two specimens of a 35 mm maximum length (Kay and Young 1969). These radulae do not change the overall variation described above: the maximum number of rows is 30, and the maximum number of teeth per row is 40. The individual variation of the features of the reproductive system is addressed in the description. The only variation that seems to be correlated to geographical distribution is the presence/absence of a muscular wall. The latter is consistently present in Australian waters: only three (out of 22) specimens from New South Wales did not have a distal muscular wall (AM C155707 #1, NMV F86423, AM C132978 #1). However, a distal muscular wall is commonly absent in specimens from Papua New Guina: four (out of nine) specimens from Papua New Guinea did not have a muscular wall (CASIZ 068283, CASIZ 068753 #1, CASIZ 071610, CASIZ 072829). The variation of the penial shape is not correlated with geographical distribution: e.g., the shape of the penis of a specimen from New South Wales (AM C123599) is much closer to the shape of the penis of a specimen from Tanzania (CASIZ 099332) than to several other Australian specimens.

DIAGNOSTIC FEATURES.— The specimens redescribed here are part of the widely-distributed species *Tayuva lilacina* because they can hardly be distinguished morphologically or anatomically from animals found in other regions. However, some subtle differences in the general organization of the reproductive system may be mentioned: the relative size of the spermatic pouches is in average higher in specimens from the eastern Pacific than in specimens from the Indo-West Pacific; also, the muscular wall seems to be less strong in specimens from the Indo-West Pacific (where it usually only protects the penial sheath) than in the three otherregions (where it often surrounds the entire distal area of the reproductive system). However, the limited number of specimens available from the Mediterranean and the Caribbean prevented addressing these differences as thoroughly as needed. Besides, such differences probably are too subtle and difficult to observe to be used as diagnostic features. Finally, these differences would not be useful in specimens that lack a muscular wall.

In the Indo-West Pacific region, distinguishing *lilacina* from *Sebadoris fragilis* should no longer be an issue, at least in most cases. Specimens longer than 80 mm alive, or with a dark ground color of the dorsal surface, or with large brown spots (that may or may not form a regular ring around the foot) on the ventral surface, are very likely not part of *lilacina*. However, younger specimens of *fragilis* with a light dorsal notum and only small spots on the ventral surface may be confused with *lilacina*.

Internal anatomy provides a clear-cut distinction between the two entities. The best internal characters to distinguish *lilacina* from *fragilis* are in the reproductive system. No distal muscular wall was found in *fragilis* (although the muscular wall is not always present in *lilacina*). The proximal part of the deferent duct of *fragilis* is not significantly folded or wider than usual, whereas it is distinctly wide in *lilacina*; the fertilization duct of *fragilis* presents a distinct organization (that certainly is its best diagnostic character) which was never found in *lilacina*. More importantly, the penis of *fragilis* is a simple, short conical papilla that cannot be confused with the penis of *lilacina*.

The notum of *fragilis* includes a thin skin and an internal, thick, muscular layer that may be easily separated; as a matter of fact, preservation separates the skin from the internal muscular layer in most specimens: this internal, muscular layer is not always present in *fragilis*, but was never found in *lilacina*. The intestine of *fragilis* is, in most individuals, not straight: it presents a long, tight loop on the right side of the digestive gland. The caecum of *fragilis* is significantly larger than in other species (not in all specimens though). Other anatomical differences between *fragilis* and *lilacina*, especially in the radula, are discussed in great detail in the re-description of *fragilis* (see this species). Finally, as shown by misidentifications found in the literature, on the *www*, or in museum collections, the other species with which *lilacina* may possibly be confused are: *Discodorididae coerulescens*, *Peltodoris murrea*, and even *Sebadoris nubilosa*. The present study provides several clear-cut features to distinguish all these entities (see those species).

Discussion.— On the one hand, the present re-description of *lilacina* specimens from the Indo-West Pacific helps address the distinction between *Sebadoris fragilis* and *lilacina*. On the other hand, it complicates the situation by showing that: 1) *lilacina* specimens from the Indo-West Pacific cannot be distinguished morphologically from *lilacina* specimens from the other regions; and 2) *lilacina* possibly is a species complex, including a few cryptic species.

All the specimens dissected for the present study (without the specimens listed as problematic) are part of a single entity. Of course, variation exists (e.g., color, radulae, relative size of spermatic pouches, penial morphology), but it is infra-specific. Clearly, the name *fragilis* applies to another entity (types were re-examined; see *fragilis*). The external morphology, especially the color, of *lilacina* fits well within the variation describe here. Also, *lilacina* is known to be common in Hawaii (although specimens from there were traditionally referred to as *fragilis*), which explains why Gould originally described it from Hawaii in 1852.

Discodoris palma has to be regarded as a synonym of *Tayuva lilacina* because no noticeable differences could be found between the specimens collected from the coasts of New South Wales (type locality of *palma*) and the rest of the specimens dissected. Of course, this does not mean that the specimens from New South Wales (up to 35° S) cannot be part of a distinct species, but, rather, at present, they cannot be distinguished. Note that Allan (1950) mentioned the existence of *palma* a few years later in a book on Australian Shells. His general description of the color ('ground color from creamy-white, pale grey, to dark rock') suggests that it is possible that Allan also regarded small specimens of *fragilis* as *palma*. This, however, does not really matter because the holotytype of *palma* is clearly not part of *fragilis*. The specimens identified as *Discodoris palma* by Thompson (1969, 1975) have outermost teeth and acidic secretion (Avila 1995) typically found in *Geitodoris*. Thompson's misidentification led Miller (1996) to propose that *palma* might belong to *Geitodoris*, which is not correct. Thompson's records of *palma* as records of *lilacina* is not accepted here. Finally, the identification of *palma* specimens from Singapore by Lim and Chou (1970) is doubtful; they likely observed *Peltodoris murrea* specimens (see this species).

The synonymy of *ketos juva* with *lilacina* is well supported. Marcus and Marcus described all the features that are found in the reproductive system of *lilacina*, especially the distal muscular wall (which the Marcus were the first to describe). The shape of the penis is unclear, but its size (1/0.2 mm) fits perfectly within the variation observed here.

Several records of *lilacina* from the literature are regarded as correct here. The specimens described by Kay and Young as *Discodoris fragilis* from Hawaii fit well within the description here, especially for the color of the dorsal notum (Kay and Young 1969: fig. 19) and the radular formula (35 mm long specimens of *fragilis* would have more than just 28/30 teeth per row). Kay and Young probably missed the distal muscular wall. A few years later, Kay (1979) mentioned the presence of *fragilis* (i.e., *lilacina*) in Hawaii, with no addition or description of new material though. The 20 mm long specimen from the Gulf of Aqaba, Red Sea, identified as *Discodoris concinna* by Engel and van Eeken (1962) probably were *lilacina*, although it is difficult to determine what the authors actually saw.

Finally, several pictures of sea-slugs published under different names are regarded here as potential records of *lilacina*. Because these records are only based on similarity of the dorsal color, they should not be regarded as certain (especially because several cryptic species might be present in the *lilacina* complex, see below): two pictures of *Discodoris fragilis* from Hawaii (Bertsch and Johnson 1981:41, unnumbered figures); a picture of *Discodoris palma* from Moreton Bay, southern Queensland (Willand and Coleman 1984:36, fig. 111); a picture of *Discodoris fragilis* from Samoa (Madrigal 1999:66, unnumbered figure); a picture of *Discodoris palma* from Heron Island, Queensland (Marshall and Willan 1999:74, fig. 125); three pictures of *Discodoris lilacina* from southern Japan (Ono 1999:104, fig. 167; Suzuki 2000:96, fig. 141; Coleman 2001: 56, unnumbered figure); one picture of *Discodoris* sp. A, from Bali, Tulamben, (Tonozuka 2003:109, fig. 140).

Problems arise when problematic specimens are considered. Indeed, those specimens have an anatomy similar to that of *lilacina*, with the exception of the penis. There are three main possible explanations for the existence of such peculiar penial morphologies. First, all specimens, including the problematic ones, are part of a single entity. Second, there is a widespread, common species (in the Indo-West Pacific) and several cryptic, rare entities, related to the widespread entity but different from it. Third, there are multiple entities, all closely related but distinct, and respectively distributed in different regions, e.g., western Indian Ocean, Papua New Guinea, and Polynesia. Because morphology reached its limits here, new kinds of data are needed to address this question. Phylogeography could show whether *lilacina* is a single unit or a species complex with several cryptic, rare species, with distinct copulatory organs.

Although penial morphology is a powerful taxonomic character at the species level, it also is problematic because: 1) atypical forms do not seem to be uncommon, and 2) are difficult to handle. For example, a specimen of *Discodorididae coerulescens* from New Caledonia has a peculiar, atypical penis that, interestingly, presents conical appendages similar to that of a problematic specimen described here (CASIZ 069742 #3). A second, smaller specimen was dissected from the same locality: both specimens have exactly the same internal anatomy, except that the penis of the second specimen is smooth. This case suggests that dissecting multiple specimens of the same species, especially from the same population/locality, may lead us to discover variants that do not fit within our typical idea of a given structure. The few problematic specimens may thus simply be individual, natural variants one finds when many specimens are fully dissected (in this case ~60).

Finally, possible affinities and synonymies with *lilacina* are discussed in the present redescription of other species (see, e.g., *Discodorididae concinna*, *Sebadoris fragilis*, *Discodorididae muta*).

Future studies.— Clearly there still is a lot to do with the taxonomy of *lilacina*: is it a single species with a highly variable penial morphology, or is it a species complex including several cryptic species hardly distinguishable with morphology? These questions can only be addressed through an integrative approach with both morphological and non-morphological data.

Tayuva lilacina (Gould, 1852)

Region: Mediterranean and eastern European Atlantic
Figures 134-141.

Discodoris maculosa Bergh, 1884b:658-662, plate LXIX, figs 8-18.— Vayssière, 1913:320.— Pruvot-Fol, 1954a:273, fig. 108.— Sordi and Majidi, 1955:240.— Swennen, 1961:62-64, figs 13e-h.— Schmekel, 1968:115.— Schmekel, 1970:197, figs 57c, 58.— Nordsieck, 1972:62.— Schmekel and Portmann, 1982:83-84, plate 30, fig. 13.— Ballesteros, Llera and Ortea, 1985:230-235, 245, figs 2-5.— Ballesteros et al., 1986:51.— Marin and Ros, 1987:141.— Cattaneo-Vietti et al., 1990:85, plate 5, fig. 5.— Trainito, 2003:36, figs 92-93. **New synonym.**

Tayuva maculosa.— Dayrat and Gosliner, 2005:202, 203, 205, 208, 209, 218, 220, 223.

Discodoris concinna.— Barash and Danin, 1977:98.— Barash and Danin, 1982:107.— Barash and Danin, 1987:133 [not *concinna* Alder and Hancock, 1864].

Discodoris confusa Ballesteros, Llera & Ortea, 1985:236-245, figs 6-8, 10C.— Wirtz, 1999:13.— Malaquias et al., 2001:78, 80-81, fig. E. **New synonym.**

Discodoris fragilis.— Ortea & Bacallado, 1981:776, plate I, fig. D.— Ortea, Bacallado, and Perez Sanchez, 1981:231-236.— Wirtz, 1995:121 [not *fragilis* Alder and Hancock, 1864].

Discodoris lilacina.— Valdés and Templado, 2002:28-30, figs 2C-D, 4.

Type material (*maculosa*).— Holotype (ZMUC GAS-2131), by monotypy: one specimen 44/29 mm preserved, [leg. unknown], May 1882.

Type material (*confusa*).— Holotype (MNHN, no catalogue number), by original designation: one specimen 30/19 mm preserved, [leg. not specified], 8 March 1980. In addition, a few paratypes were deposited at the Departamento de Zoologia of the Universidad de La Laguna, Spain. The paratypes were not re-examined for the present study.

Type locality (*maculosa*).— Near Naples, [Italy, Mediterranean Sea].

Type locality (*confusa*).— Las Caletas, [28°58′N, 13°31′W], Lanzarote, [Canary Islands, eastern Atlantic Ocean]. This is the locality of the holotype. Ballesteros and co-authors cited three additional localities from the Canary Islands for the paratypes: Isla de Tenerife (7 individuals), Isla de La Palma (2 individuals), Isla de Gran Canaria (3 individuals).

Type material condition (*maculosa*).— The holotype was entirely dissected by Bergh. Only the body wall and the gills remain.

Type material condition (*confusa*).— The holotype, globally well preserved, was not dissected, but was open on the lateral side.

Additional material dissected.— [**Mediterranean Sea**, Spain], Almeria, Los Escullos, 30°48′N, 2°04′W, one specimen 30/ 17 mm preserved, 25 January 1990, 1 meter depth, leg. J. Templado, identified as *Discodoris maculosa* by J. Templado (MNCN 15.05/801) [the penis, drawn, was lost during SEM preparation]; [Mediterranean Sea, Spain], Granada, Malaga, Cala Vaca, Cerro Gordo, one specimen 38/28 mm preserved, 12 June 1993, leg. J. Templado, identified as *Discodoris maculosa* by J. Templado (MNCN

15.05/17.769); [Mediterranean Sea, Spain], Almería, Los Escullos, one specimen 24/16 mm preserved, 16 October 1990, leg. J. Templado, identified as *Discodoris maculosa* by J. Templado (MNCN 15.05/867); Mediterranean Sea, Lebanon, El Heri, 2-3 m depth, 3 June 2000, one specimen 23/12 mm preserved length, leg. H. Zibrowius, identified as *Discodoris lilacina* by A. Valdés and J. Templado (LACM 152717) [this specimen was dissected prior to the present study by Valdés and Templado (2002); the labial cuticle and the radula, which did not accompany the specimen, could not be re-examined]; [**Atlantic Ocean**, Canary Islands], Kanariske Øer, Tenerife, Puerto de la Cruz, one specimen 37/23 mm preserved, Tidevanszonen [tidal zone], 4 March 1947, leg. [Gunnar] Thorson, unidentified (ZMUC, no catalogue number).

DISTRIBUTION.— So far, *lilacina* has been recorded from several localities from the western Mediterranean Sea, on the coasts of Spain, France, and Italy (Bergh 1884b; Schmekel 1968; Schmekel and Portmann 1982; Ballesteros et al. 1985, 1986; Cattaneo-Vietti et al. 1990; present study). It has been recorded from the eastern Mediterranean Sea as well, on the coasts of Turkey and Lebanon (Swennen 1961; Valdés and Templado 2002); also, the records of *concinna* from the Mediterranean coasts of Israel (Barash and Danin 1977, 1982, 1987) are regarded here as records of *lilacina* (see discussion). Finally, it has been recorded from the Canary Islands (Ortea and Bacallado 1981, as *fragilis*; Ortea et al. 1981, as *fragilis*; Ballesteros et al. 1985, as *confusa*; present study) and Madeira (Wirtz 1995, as *fragilis*; Wirtz 1999, as *confusa*; Malaquias et al. 2001, as *confusa*). Note that *lilacina* is cited under three names (*Discodoris fragilis*, *Discodoris maculosa*, and *Discodoris confusa*) in the European Register of Marine Species (Costello et al. 2001).

WWW.— The specimen photographed from Granada, Spain, by Luiz Sanchez Tocino, and identified as *Discodoris fragilis* probably is part of *lilacina* (website: Opisthobranquios de la Costa de Granada). The 50-70 mm long (alive) specimen photographed by Ferda Buyukbaykal from Cesme-Izmir, Turkey, at 8-10 meters depth, in June 1998, and identified as *Discodoris lilacina*, probably is part of *lilacina*.

OCCURRENCE.— Given the number of specimens found in collections or mentioned in the literature and the number of pictures posted on the *www*, *lilacina* does not seem to be rare in the Mediterranean and eastern European Atlantic.

HABITAT.— Most specimens were collected under stones, from the intertidal zone up to 24 meters depth (Swennen 1961; Ballesteros et al. 1985; Wirtz 1995).

LITERATURE.— Most authors have provided general information about the color and the general morphology (Bergh 1884b; Swennen 1961; Schmekel and Portmann 1982; Ballesteros et al. 1985, as *maculosa* and *confusa*; Cattaneo-Vietti et al. 1990; Wirtz 1995, as *fragilis*; Wirtz 1999, as *confusa*; Malaquias et al. 2001, as *confusa*; Valdés and Templado 2002; Trainito 2003). Several authors have mentioned radular features (Bergh 1884b; Pruvot-Fol 1954a; Swennen 1961; Schmekel and Portmann 1982; Ballesteros et al. 1984, as *maculosa* and *confusa*; Cattaneo-Vietti et al. 1990; Valdés and Templado 2002). Also, a few authors have described and illustrated the reproductive system (Bergh 1884b; Schmekel and Portmann 1982; Ballesteros et al. 1984, as *maculosa* and *confusa*; Valdés and Templado 2002). However, those descriptions are confusing: only Schmekel and Portmann (1982) represented a reproductive system that is close to the reality (although they did not describe the shape of the penis); the other descriptions of the reproductive system are incomplete or erroneous (see below). Finally, the intra-specific variation of anatomical characters has never been addressed.

Note that Pruvot-Fol (1954a) simply translated Bergh's description of *maculosa* and used his figures, but did not add new data. Marcus and Marcus (1967a) briefly mentioned the existence of *lilacina* (as *maculosa*) as a Mediterranean species, without discussing its status or adding new data. Finally, note that several authors have recorded the presence of this species from different Mediterranean localities, but without describing the animals they were referring to (Sordi and Majidi 1955; Schmekel 1968; Ballesteros et al. 1986; Marin and Ros 1987).

Remarks on the original description (*maculosa*, Figs. 134A-B, D).— The ground color of the dorsal notum of the preserved holotype is creamish, with darker brown irregular spots and blotches, among which two longitudinal rows cannot really be recognized; the ventral side is also creamish with dark dots. A piece of the notum of the holotype was prepared for SEM, but the notum was too poorly preserved and it did not provide any information. Bergh described several important characters, such as the bilabiate anterior foot with the superior lip notched, and the presence of digitiform oral tentacles. The labial cuticle is armed. The radular formula was 40 × (43/46-0-43/46) in a 44 mm long preserved specimen (48 mm according to Bergh). Bergh also mentioned the presence of tiny conical elements along the rachidian axis. Those elements probably are the remnant of rachidian teeth (they can occasionally be observed in specimens). Contrary to what Marcus and Marcus (1967a) stated, the presence of those structures should not constitute a diagnostic character for *maculosa*. Bergh accurately described and represented the longitudinally folded proximal part of the deferent duct. However, he misinterpreted it as part of the prostate. Bergh also described a structure that could be interpreted as a muscular wall around the penis, but he unfortunately did not draw it.

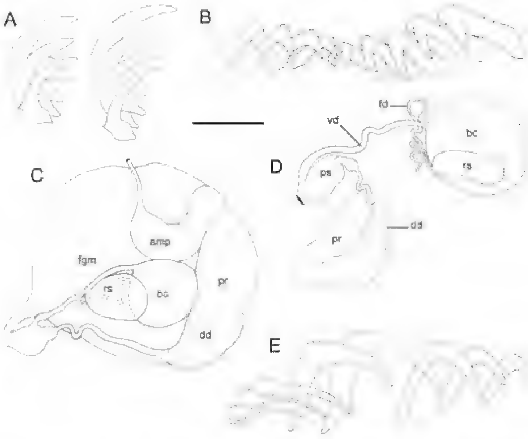

Figure 134. *Tayuva lilacina* (Mediterranean & eastern Atlantic), original descriptions. A. Outermost teeth of *Discodoris maculosa*, after Bergh (1884b: plate LXIX, fig. 17).— B. Innermost teeth of *Discodoris maculosa*, after Bergh (1884b: plate LXIX, fig. 11).— C. Reproductive system of *Discodoris confusa*, after Ballesteros et al. (1985: fig. 7H), scale = 4 mm.— D. Part of the reproductive system of *Discodoris maculosa*, after Bergh (1884b: plate LXIX, fig. 18).— E. Lateral teeth (#38, 37, 36, 33, 24, 5, 3, 1) of *Discodoris confusa*, after Ballesteros et al. (1985: fig. 8), scale = 75 μm.

Remarks on the original description (*confusa*, Figs. 134C, E).— Ballesteros and co-authors provided a thorough description of the external morphology, including the color of the dorsal notum (dorsal background light grey or creamy-grey, with blotches of various colors –from whitish to black- irregularly distributed, although the median part of the dorsal notum tends to be darker). The dorsal surface of the preserved holotype is dirty creamish-grayish, with a few traces of darker spots. The ventral surface is creamish, with no dots. Ballesteros and co-authors mentioned that they dissected four specimens, but only two radular formulae are provided: 28 × (38-0-38) in a 55 mm long individual, and 30 × (43-0-43) in a 65 mm long individual. The intestine that they represented is not straight but presents a loose lateral loop (on the right side of the digestive gland). The intestine of the holotype, re-examined for the present study, is straight. The authors misinterpreted the folded proximal part of the deferent duct as a distal part of the prostate. Also, more importantly, a muscular wall in the distal part of the reproductive system, not mentioned by the authors in the original description, is clearly present in the holotype. Since the authors asserted that they dissected four specimens, it is likely that they overlooked this muscular wall. Indeed, it was observed in all the specimens dissected. Although this structure may be absent in some individuals, it is unlikely that the four specimens dissected by the authors had no muscular wall. The authors did not describe the shape of the penis, a key taxonomic character. Finally, the characters that the authors provided to distinguish *confusa* from *lilacina* (as *maculosa*) are not valid (due to some individual variation not considered by the authors; see discussion). In any case (see discussion), comparing *confusa* (and *maculosa*) with *fragilis*, an Indo-Pacific species, is not really interesting because *fragilis*, which belongs to *Sebadoris*, is not closely related to *maculosa* (= *lilacina*).

Description of new specimens (Figs. 135-141).— *Color*. Unfortunately, no information about the color of live animals was available for the individuals dissected in the present study. The ground color of the dorsal notum of preserved specimens is creamish with some brown spots, among which two longitudinal rows of darker spots (from the rhinophores to the gills) may or may not be recognizable. The ventral surface (hyponotum and foot) bears dark brown dots.

External morphology. The body is oval. The length equals less than twice the width. The largest specimen was 38 mm long, preserved. The foot is rounded posteriorly and anteriorly. The width of the foot equals about one third or one half the width of the dorsal notum (in preserved specimens). The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, but not grooved. The dorsal notum bears tubercles that are not caryophyllidia. Many small holes (diameter < 10 µm) and many tufts of cilia were found on the surface of the dorsal notum (including the gills and the rhinophores). Tubercles have an apex entirely covered with cilia, which makes them look like caryophyllidia, but without a regular crown of protruding spicules. In preserved specimens, the margins of the rhinophoral and branchial sheaths can be smooth or crenulate. There are six wide tetra- or tripinnate branchial plumes arranged in circle around the anus. The rhinophores have from 13 to 30 lamellae, depending on the size of the animal.

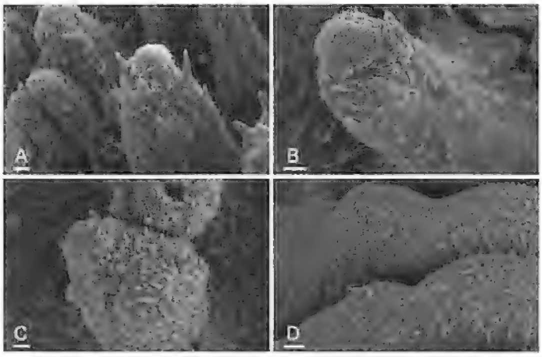

Figure 135. *Tayuva lilacina* (Mediterranean & eastern Atlantic), notum and rhinophores. A. Dorsal notum, MNCN 15.05/801, scale = 20 µm.— B. Dorsal notum, MNCN 15.05/801, scale = 20 µm.— C. Dorsal notum, MNCN 15.05/17.769, scale = 20 µm.— D. Rhinophoral lamellae, MNCN 15.05/801, scale = 20 µm.

Digestive system. The stomach is large, free, on top of the left anterior side of the digestive gland. A small caecum is located on the left posterior side of the stomach (a caecum could not be observed in the specimen from Tenerife). The intestine is straight and dorsal. The labial cuticle is armed with a pair of jaws constituted by rodlets. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. Radular formulae were: 17 × (24-0-24) in a 24 mm long specimen (MNCN 15.05/867), 18 [some rows had probably been lost] × (34-0-34) in a 37 mm long specimen (ZMUC, Tenerife), 25 × (33-0-33) in a 30 mm long specimen (MNCN 15.05/801), and 26 × (31-0-31) in a 38 mm long specimen (MNCN 15.05/17.769). The rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the six or eight innermost teeth of which the size increases gradually and the four or six out-

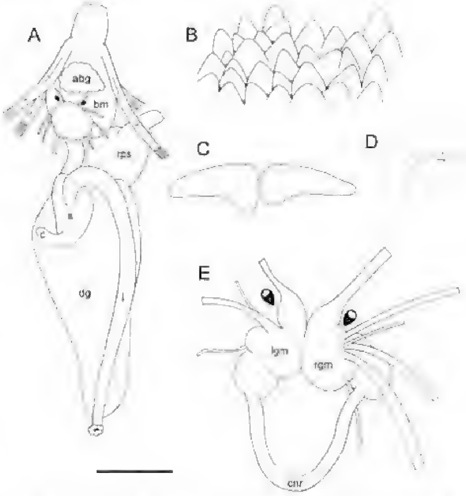

Figure 136. *Tayuva lilacina* (Mediterranean & eastern Atlantic), MNCN 15.05/801. A. General anatomy, scale = 5 mm.— B. Dorsal tubercles, scale = 0.85 mm.— C. Jaws, scale = 1 mm.— D. Anterior, ventral view, scale = 10 mm.— E. Nervous system, scale = 1 mm.

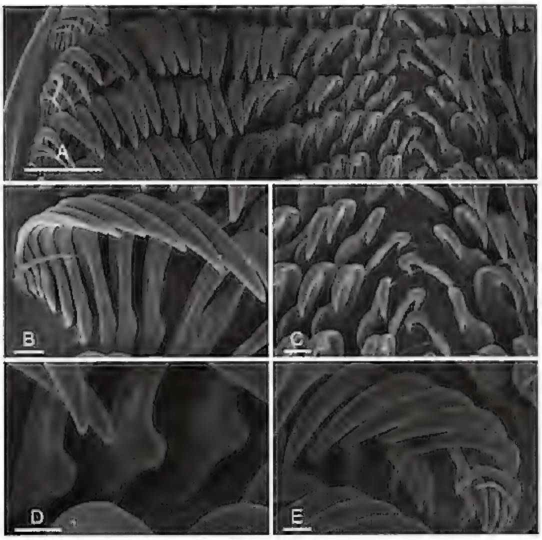

FIGURE 137. *Tayuva lilacina* (Mediterranean & eastern Atlantic), radula. A. Left rows, MNCN 15.05/867, scale = 100 µm.— B. Outermost teeth, MNCN 15.05/867, scale = 20 µm.— C. Innermost teeth, MNCN 15.05/867, scale = 20 µm.— D. Median teeth, detail, ZMUC, scale = 30 µm.— E. Outermost teeth, ZMUC, scale = 30 µm.

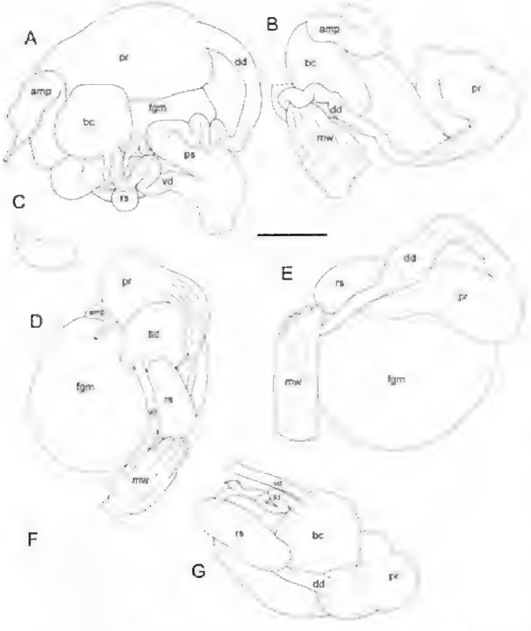

FIGURE 139. *Tayuva lilacina* (Mediterranean & eastern Atlantic), reproductive system. A. LACM 152717, after Valdés and Templado (2002: fig. 2A).— B. LACM 152717 (same specimen as in A), scale = 1 mm.— C. Penis, LACM 152717 (same specimen as in A), scale = 1 mm.— D. ZMUC, scale = 3 mm.— E. ZMUC, scale = 3 mm.—. F. Penis, ZMUC, scale = 1 mm.— G. Spermatic ducts, ZMUC, scale = 3 mm.

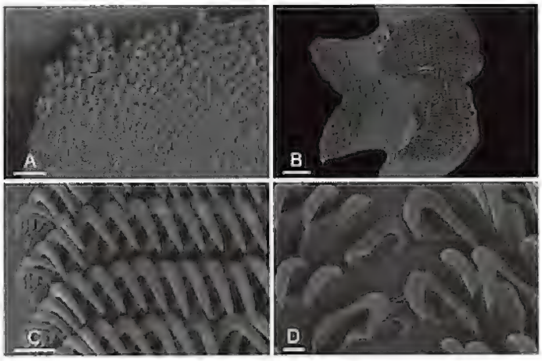

FIGURE 138. *Tayuva lilacina* (Mediterranean & eastern Atlantic), radula and labial cuticle, MNCN 15.05/801. A. Jaw rodlets, scale = 20 µm.— B. Radula, scale = 400 µm.— C. Outermost teeth, scale = 100 µm.— D. Innermost teeth, scale = 20 µm.

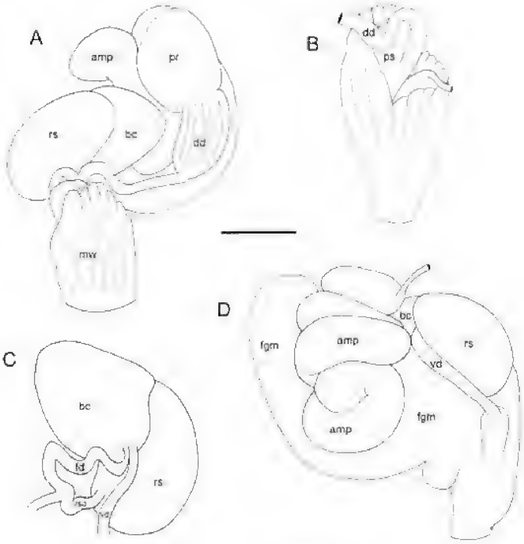

FIGURE 140. *Tayuva lilacina* (Mediterranean & eastern Atlantic), MNCN 15.05/801, reproductive system. A. Scale = 1.5 mm.— B. Distal muscular wall, scale = 1.2 mm.— C. Spermatic pouches and ducts, scale = 1.7 mm.— D. Scale = 1.7 mm

ermost ones of which the size decreases gradually. All teeth are hamate, including the outermost ones, although the base of the last outermost tooth can be reduced. The teeth are not grooved and bear no denticles. However, the base of the teeth of the specimen from Tenerife (ZMUC) bear a distinct spur that was not found in other radulae.

Nervous system. The length of the circum-

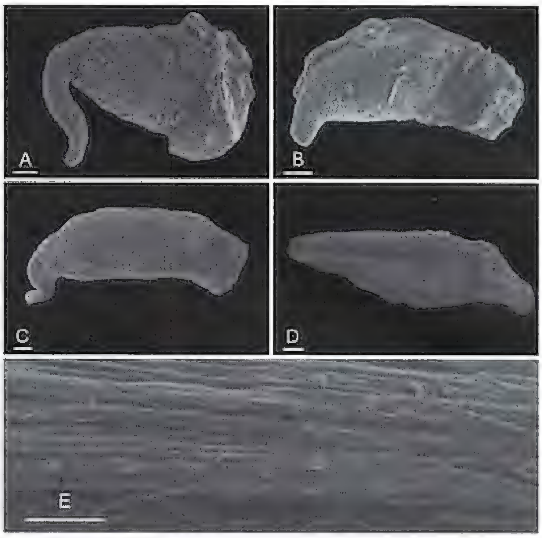

FIGURE 141. *Tayuva lilacina* (Mediterranean & eastern Atlantic), penis. A. MNCN 15.05/17.769, scale = 100 µm.— B. LACM 152717, scale = 100 µm.— C. ZMUC, scale = 100 µm.— D. Distal muscular wall, MNCN 15.05/801, scale = 200 µm.— E. Distal muscular wall, detail, MNCN 15.05/801, scale = 100 µm.

esophageal nerve ring equals two or three times the width of the cerebro-pleural ganglia. The cerebral and pleural are fused, but separate from the pedal ganglia. Their surface is smooth.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla makes several tight loops. The division between male and female ducts (in the female gland mass) could not be seen by dissection. The prostate is divided in a proximal whitish part and a distal yellowish-orange part. Occasionally (e.g., ZMUC), a third, additional part is distinguishable within the second prostatic part, near the deferent duct. The deferent duct is short. It can be straight or loosely convoluted (from one to a few loops). More importantly, its proximal part, near the prostate, is wide (much wider than usual) and folded longitudinally; the folds are internal but recognizable externally. The deferent duct ends in a distinct penis (which is not just the evaginable distal part of the deferent duct). It presents a basal part that is more or less cylindrical, with an elongated, narrow, apical tail. The penis could not be found in one of the Mediterranean specimens (MNCN 15.05/867) because the reproductive system, small, was probably not mature. Also, the penis of another Mediterranean specimen (MNCN 15.05/801) was long and narrow, with a short base. The vaginal duct is straight. The deferent duct and the vaginal duct join to form a vestibule that may or may not remain separate from the female duct. More importantly, a strong muscular wall protects the distal area of the reproductive system. The muscular wall can surround entirely the distal area or be just on one side (the dorsal side). The fertilization duct is short. It presents one or two loose loops near the bursa copulatrix (e.g., ZMUC, MNCN 15.05/801), or is straight (e.g., MNCN 15.05/17.769). The connection between the fertilization duct and the female gland mass is marked by a distinct duct. The duct of the receptaculum seminis is short but distinct too. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is underneath the receptaculum seminis and the bursa copulatrix. The bursa copulatrix can be slightly larger (MNCN 15.05/801), two or three times larger (ZMUC), or up to ten times larger (MNCN 15.05/867) than the receptaculum seminis. Both spermatic pouches are spherical-ovate and smooth, although the receptaculum may be more elongated.

INFRA-SPECIFIC CHARACTER VARIATION.— Anatomical and morphological data available in the literature are largely congruent with the present redescription. The largest, living animals known are 80 mm long (Ballesteros et al. 1985, as *confusa*) and 60 mm long (Swennen 1961). The largest preserved animals known are 52 mm long (Ballesteros et al. 1985, as *maculosa*) and 48 mm long (Bergh 1884b, holotype of *maculosa*). Radular formulae found in the literature are (in addition to the formulae from the original descriptions): 20 × (22-0-22) in a 23 mm long specimen (Valdés and Templado 2002, as *lilacina*), 11 × (25-0-25) in a 30 mm long specimen (Ballesteros et al. 1985), 37 × (40-0-40) in a 60 mm long living specimen (Swennen 1961), and 23 × (42-0-42) in a 35 mm long specimen (Schmekel and Portmann 1982). Overall, the number of rows varies from

11 (for 25 teeth per half row) up to 40 (for 43/46 teeth per half row), and the number of teeth per half row varies from 22 (for 20 rows) to 43/46 (for 40 rows). The presence of a well-marked spur on the base of the teeth of the specimen from Tenerife (ZMUC) can be easily explained by individual variation: the original description of *confusa* did not mention the presence of such a spur.

Diagnostic features.— The specimens redescribed here are part of the widely-distributed species *Tayuva lilacina* because they can hardly be distinguished morphologically or anatomically from animals found in other regions.

Discussion.— First, here is discussed the synonymy of *confusa* with *lilacina*, i.e., the absence of distinction between *confusa* and what was referred to for a long time as *Discodoris maculosa*. The characters that Ballesteros and co-authors (1985) provided to distinguish *confusa* from *maculosa* (dorsal tubercles closer and more uniform, no autotomy of the notum, bursa copulatrix white, and 'different' jaws elements) should not be used in alpha-taxonomy because of a great deal of individual variation. The abundance and the shape of tubercles even vary on the dorsal notum of a single individual (e.g., tubercles present on the edges of the notum *versus* tubercles present in the middle of the notum). The autotomy of the notum, which has been observed in many species, is by no means a "specific" feature but rather a phenomenon that may occasionally occur in individuals of discodorid species under certain conditions.The color of the bursa copulatrix may change during the life of individuals when the spermatic content changes; also, the color of the bursa copulatrix (as well as all internal organs in general) greatly depends on preservation. Finally, the shape of the rodlets varies depending on the usage of the jaws by the animals; the same jaw may include rodlets whose apex can be round *and* pointed: in fact, most often, the apex of the rodlets is destroyed and shapeless.

Ballesteros and co-authors compared *Discodoris confusa* with *Discodoris fragilis* (based on specimens that Edmunds sent them from Tanzania). This comparison is actually less informative and needed than what the authors were thinking. Comparing *confusa*, which belongs to *Tayuva*, with *Sebadoris fragilis* necessarily makes *confusa* a "different" species because *fragilis* is distinct from *maculosa-confusa* (= *lilacina*). The authors should have compared their *confusa* with specimens of the same species complex, or at least genus, i.e., specimens of *Tayuva lilacina* from the Indo-West Pacific too, but anatomically similar to *maculosa*. Note that the drawings published by Ballesteros and co-authors (in particular the reproductive system) show that the specimens that Edmunds sent them from Tanzania really were part of *Sebadoris fragilis* and not *Tayuva lilacina*.

More importantly, Ballesteros and co-authors have overlooked some critical anatomical features shared by all individuals from the Mediterranean Sea (which they called *maculosa*) and the Canary Islands (which they called *confusa*). In particular, they did not describe the muscular wall in the distal part of the reproductive system: this structure is clearly present in the holotype of *confusa* (see remarks on the original description). They also did not pay attention to the folded proximal part of the deferent duct (although they represented it), which was observed in all specimens dissected here, including the holotypes of *confusa* and *maculosa*. However, these two structures are also found in all specimens of *Tayuva lilacina* around the world, and therefore are not diagnostic of "*maculosa*." The specimen from the Canary Islands (which has the same anatomy as the holotype of *confusa*) has the exact same penis as the specimens from the Mediterranean Sea (Spain and Lebanon). In conclusion, the morphological data currently available do not support the idea that '*maculosa*'-like individuals from Madeira and the Canary Islands are part of an entity distinct from the Mediterranean individuals, but phylogeography may demonstrate in the future that they form a distinct unit.

A manuscript written by Vérany in the 1850s and recently published (Vérany 2001), indicates that Vérany had already named *lilacina* animals from the Mediterranean (= *maculosa*) as *Doris*

DelleChiaje. The color drawing of a live animal prepared by Vérany (2001: plate 2, fig.11) is similar to *lilacina*.

Another important issue is the identity of *maculosa*-like specimens from the eastern Mediterranean Sea. In 1961, Swennen recorded *lilacina* (as *maculosa*) from the coasts of Turkey and rightly pointed out that this species had not been found since Bergh's original description in 1884. Then, in three publications, Barash and Danin (1977, 1982, 1987) identified specimens from the Mediterranean coasts of Israel as *Discodoris concinna*, a name normally used for species (more than one) from the tropical Indo-West Pacific. By the name *concinna*, they were probably referring to either young specimens of *Sebadoris fragilis* or specimens of *Tayuva lilacina*. However, Barash and Danin did not mention the existence of a similar-looking, native Mediterranean species, *maculosa*, known from Turkey since Swennen (1961). Given that *maculosa* is not distinguishable from *lilacina*, at least at present, and that distinguishing *maculosa* from young specimens of *fragilis* requires a dissection (the color of the ventral surface also distinguishes these two species), it is possible that Barash and Danin collected specimens of *lilacina* (which in the Mediterranean authors refered to as *maculosa*). It seems simpler to accept that a native Mediterranean species was overlooked and misidentified, than having to explain the presence of these specimens through a Lessepsian migration.

More recently, Valdés and Templado (2002) identified a specimen from the coasts of Lebanon as *Discodoris lilacina* and argued that the presence of *lilacina* in the Mediterranea Sea was another case of "Lessepsian" immigrant species (from the Indo-West Pacific). Because Valdés and Templado (2002: p. 29) strongly asserted that they had "*no doubt* about the identity of the Lebanese specimen," *lilacina* was mentioned by Zenetos and co-authors (2003) as one of the non-indigenous Mediterranean species in their *Atlas of exotic species in the Mediterranean*. According to Valdés and Templado, they presented "the first confirmed Mediterranean record for *D. lilacina*." However, Valdés and Templado did not mention the existence of *maculosa* (i.e., name used since the 19th century for *lilacina*) in the eastern Mediterreanean, although they mentioned *confusa* from the Canary Islands and Madeira. Re-examination of the specimen dissected by Valdés and Templado (LACM 152717) has demonstrated that these authors missed: the muscular wall around the distal part of the reproductive system, and the wide, folded, proximal part of the deferent duct. Consequently, based on the description provided by Valdés and Templado, this specimen from Lebanon is very different from *lilacina*, and should not even belong to *Tayuva*. Also, the authors did not describe the penis. Once the anatomy of this specimen is corrected, it then becomes indeed identical to the specimens of *lilacina* from the Indo-West Pacific... as well as from the rest of the world, including the Mediterranean, where *lilacina* was referred to as *maculosa*.

Although this Lebanese specimen and, possibly, the specimens collected from Israel by Barash and Danin, are part of *lilacina*, we do not know whether they are more closely related to the tropical Indo-West pacific populations orthe Mediterranean populations of *lilacina*. Individuals from eastern Mediterranean could be part of a "maculosa" species in the Mediterranean and eastern Atlantic, but they could also be part of a different species, *lilacina*, exclusively represented in the Indo-West Pacific, and thus be representatives of "Lessepsian immigrants." However, because, again, the taxonomy of the species complex *Tayuva lilacina* is not solved based on morphology, at present, this question cannot be addressed. Three points can be mentioned, however. First, *lilacina* is less common in western Indian Ocean than what is commonly thought. As a matter of fact, the records of "*concinna*" or "*fragilis*" from the western Indian Ocean or the Red Sea (the name *lilacina* has never been used for specimens from the western Indian Ocean prior to the present study) are records of *Sebadoris fragilis*, not *lilacina*; also, the most common species in western Indian Ocean is *fragilis*, not *lilacina*. Second, the Suez Canal will be an area where the sampling will be critical in order to solve whether eastern Mediterranean specimens are indigenous or Lessepsian immigrants. And, it seems that neither *lilacina* nor *fragilis* have been mentioned from the Suez Canal, which, interestingly, is a point already made by Barash and Danin (1972, 1987). Finally, *lilacina* has never been positively demonstrated to be present in the Red Sea either: all the records of *fragilis* or *concinna* in the Red Sea actually refer to *Sebadoris fragilis*. So, it is more likely that the specimens found in eastern Mediterrean are more closely related to the other Mediterranean specimens than to the Indo-West Pacific populations or species, but this needs to be verified with additional data.

Supra-specific relationships.— Dayrat and Gosliner (2005), who regarded *maculosa* and *lilacina* as two distinct species, already re-allocated them to *Tayuva*, based on a phylogenetic analysis. The same result was found here: *Tayuva* is clearly distinct from *Discodoris*. Now that only one species of *Tayuva* is regarded as valid, one might consider that *Tayuva lilacina* could simply become *Discodorididae lilacina*. However, the name *Tayuva* is used because it is likely that *lilacina* refers to a species complex, rather than a well-delineated entity. The Linnaean binomial of *lilacina* under the ICZN is *Tayuva lilacina*, which also is a possible name under the *ICPN*. If one considers all synonyms of *lilacina* and their nomenclatural history, as well as misidentifications, several supra-specific affinities have been proposed for members of *Tayuva*, which have been placed in *Discodoris*, *Peltodoris*, and *Doris*, in addition to *Tayuva* itself. Some authors (Kay 1979; Bertsch and Johnson 1981) thought that *Doris lilacina* Gould, 1852 could be a *Chromodoris*. However, Gould's drawings of the external morphology indicate that his *Doris lilacina* was not *Chromodoris*.

Sebadoris Marcus and Marcus, 1960

Under the *ICZN*, *Sebadoris* is a taxon of genus-level. Type-species: *Thordisa crosslandi* Eliot, 1903, by original designation, which is regarded as a synonym of *Sebadoris nubilosa* (Pease, 1871).

The phylogenetic diagnosis of *Sebadoris* includes three classes of characters, depending on their phylogenetic significance. 1) Two synapomorphies exclusively found in this taxon: a significantly large caecum of the stomach; a long, convoluted intestine, with a loop on the right lateral side of the digestive gland; only these synapomorophies can be regarded as diagnostic of *Sebadoris* (i.e., only this character can be used to identify that a species belongs to *Sebadoris*). 2) Four synapomorphies of *Discodorididae*: a notched upper lip of the bilabiate anterior foot, digitiform or conical oral tentacles that are *not* expansions of the lateral mouth lips, a flattened prostate divided in two parts of distinct color, and two blood glands. 3) Characters found in many other dorid nudibranchs, e.g., absence of rachidian teeth, hamate lateral teeth, etc.

In the present contribution, *Sebadoris* refers to a clade name, but is not assigned to any particular rank. Under the *ICPN*, *Sebadoris* is a converted clade name: it remains an informal clade name until it is phylogenetically defined *and* formally registered. *Sebadoris* could be phylogenetically defined through an apomorphy-based definition as "the clade stemming from the first organism or species to possess a long, convoluted intestine with a loop on the right lateral side of the digestive gland, as inherited by *Sebadoris nubilosa* (Pease, 1871)."

Sebadoris nubilosa (Pease, 1871)

Figures 142-153.

Doris nubilosa Pease, 1871:13-14, plate 6.
Discodoris ? nubilosa.— Pruvot-Fol, 1947:113.
Archidoris nubilosa.— Kay and Young, 1969:343-344, figs 6-7.— Kay, 1979:460, fig. 148.

Sebadoris nubilosa.— Edmunds, 1971:342-347, figs 2, 4A.— Marshall and Willan, 1999:84-85, figs 149-150.— Valdés, 2002:608-611, figs 34C, 42-43.— Yonow, 2008:154, four unnumbered figures.
Discodorididae nubilosa.— Dayrat and Gosliner, 2005:205.
Thordisa crosslandi Eliot, 1903:368-369, plate XXXII, fig. 3, plate XXXIII, figs 4-8.— Eliot, 1906b:656-657.— Eliot, 1910a:411, 421, plate 25, fig. 1.— Crossland, 1937:31.— Satyamurti, 1952:239-240, plate XXX, figs 1-2, plate XXXI, figs 1-5.
Sebadoris crosslandi.— Marcus and Marcus, 1960a:905-907, figs 47-54; 1970c:166.— Soliman, 1980:227-238, figs 1-10.— Soliman, 1991:260-261.
Diaulula ? *gigantea* Bergh, 1905:119-120, plate XV, figs 11-16.
Argus indicus O'Donoghue, 1932:156-158.— Satyamurti, 1952:239-240, plate XXX, figs 1-2, plate XXXI, figs 1-5.
Austrodoris ellioti.— Pruvot-Fol, 1954b:16-18, fig. 5 [not *ellioti* Alder and Hancock, 1864].

Type material (*nubilosa*).— Holotype, by monotypy. According to Kay and Clench (1975), Pease's collection is at the Museum of Comparative Zoology, Harvard. However, the type of *nubilosa* is not at the MCZ.

Type material (*crosslandi*).— The type material, which includes "many specimens" (Eliot 1903:368) collected in 1901 and 1902, could not be found. It is not at the Natural History Museum, London.

Type material (*gigantea*).— The type specimen described by Bergh (1905) is neither at the Zoölogisch Museum, Amsterdam, which holds the material from the Siboga Expedition, nor at the Zoological Museum, University of Copenhagen, which holds Bergh's personal collections. It is probably lost.

Type material (*indicus*).— Holotype, by monotypy. The type is not at the Natural History Museum, London, which holds some of O'Donoghue's collections. However, the type has no real reason to be in London: it should actually be in the collection of the Government Museum Chennai, i.e., the former Madras Government Museum. When O'Donoghue's (1932:141) description was published, the type of *indicus* was already in the possession of the Madras Government Museum. O'Donoghue had obtained this specimen from the curator of zoology of the Madras Government Museum, Dr. F.H. Gravely, who had collected many mollusks in the Gulf of Manaar. Thomas Satyamurti (1952:239), Gravely's successor at the Madras Museum, gives us some information about the history of this specimen: "This species [*Thordisa crosslandi*] is represented in the collection [of the Madras Museum] by a single large specimen collected at Kundugal Point. (…) [This specimen] was sent to Dr. O'Donoghue [Winckworth put O'Donoghue in touch with Gravely (see O'Donoghue 1932:141)] although along with other Pamban Nudibranchs and was described by him as a new species, *Argus indicus* (…); finally Col. H.C. Winckworth re-examined the same specimen, and referred to it with certainty to *Thordisa crosslandi*, under which name therefore it is recorded in the present paper." It could not be established where O'Donoghue re-examined the specimen: Madras, Edinburgh, or even the University of Manitoba, Canada, where O'Donoghue was working then. In any case, in 1952, the type of *Argus indicus* was held by the Madras Government Museum. This institution was contacted, to ask if a specimen of *Argus indicus* or *Thordisa crosslandi* was in their mollusk collection, but no answer was received. However, the type of *indicus* could still be there.

Type locality (*nubilosa*).— Huaheine [Huahine], Society Islands, French Polynesia.

Type locality (*crosslandi*).— Chuaka, East Coast of Zanzibar, Indian Ocean.

Type locality (*gigantea*).— Ruma-Kuda-Bai, Roma Island, Indonesia.

Type locality (*indicus*).— Kundugal Point [O'Donoghue spelled this locality 'Kitukal'], around Krusadai Island, Gulf of Manaar, Indian Ocean.

Additional material dissected.— **Indian Ocean**, Seychelles, Mahe Island, 1 km North of 'Fairyland,' 24 April 1984, one specimen 70/45 mm preserved, leg. T. M. Gosliner, identified as *Sebadoris nubilosa* by T. M. Gosliner (CASIZ 074202) [this specimen was dissected prior to the present study but all organs are still in the jar]; Indian Ocean, Seychelles, Aldabra Island, Passe Femme, 09°00'S, 46°00'E, 12 March 1986, one specimen 80/45 mm preserved, leg. T. M. Gosliner, identified as *Sebadoris nubilosa* by T. M. Gosliner (CASIZ 074254); Indian Ocean, Madagascar, Mora Mora Village, 5 April 1989, one specimen 65/55 mm preserved, leg. T. M. Gosliner, identified as *Sebadoris nubilosa* by T. M. Gosliner (CASIZ 070352) [the specimen was dissected prior to the present study but all organs were still in the jar]; [**Pacific Ocean**], Hawaiian Islands, Waikiki, Oahu, June 1954, two specimens 130/90 (#1) mm and 110/90 (#2) mm preserved, leg. Cutress, unidentified (NMNH 576413); [Pacific Ocean, French Polynesia, Austral Islands], Tubuai Islands, Rurutu, 1965, two specimens 60/50 (#1) and 40/30 (#2) mm preserved, leg. [R. L.] Sixberry, identified as *Sebadoris crosslandi* by Ernst and Eveline Marcus (NMNH 576435) [these specimens are vouchers of Marcus and Marcus (1970c)]; Pacific Ocean, Austral Islands, Rurutu Island, south of Avera, 28 January 1983, one specimen 85/65 mm preserved, leg. G. Paulay, identified as *Sebadoris nobilosa* by T. M. Gosliner (CASIZ 071727) [this specimen was dissected by Valdés (2002) prior to the present study; the reproductive system was still in the jar, but largely destroyed; the penis was missing; the radula was extracted by Valdés; the labial cuticle was prepared for SEM for the present study].

Distribution.— Indo-West Pacific: Red Sea (Soliman 1980, as *crosslandi*; Yonow 2008), Tanzania (Edmunds 1971, as *nubilosa*), Zanzibar (Eliot 1903, type locality of *crosslandi*), Madagascar (present study), Seychelles (Eliot 1910a, as *crosslandi*; present study), Maldives (Marcus and Marcus 1960a, as *crosslandi*), Gulf of Manaar (O'Donoghue 1932), Banda Sea, Indonesia (Bergh 1905, type locality of *gigantea*), Queensland (Marshall and Willan 1999, as *nubilosa*), Society Islands, French Polynesia (Pease 1871, type locality of *nubilosa*), Tubuai Islands, French Polynesia (Marcus and Marcus 1970c, as *crosslandi*; Valdés 2002, as *nubilosa*; present study), Tuamutu Archipelago, French Polynesia (Pruvot-Fol 1954b, as *elliotti*), Hawaii (Kay and Young 1969, as *nubilosa*; Kay 1979, as *nubilosa*; present study).

Most specimens have been collected from the eastern Indian Ocean or on the eastern borders of the western Pacific Ocean (i.e., French Polynesia, Hawaii). Records from western Pacific (Indonesia, Philippines, Papua New Guinea, etc.) are not common. As a matter of fact, no material could be dissected from those places for the present study. Outside the Indian Ocean, French Polynesia, and Hawaii, *nubilosa* has only been recorded once in Indonesia (type locality of *gigantea*), once in Mactan Island, Philippines (see the *www* section below), and once on Heron Island, Queensland (Marshall and Willan 1999). Those specimens, however, were not dissected, and our anatomical knowledge on specimens identified as *nubilosa* from places other than the Indian Ocean, French Polynesia, or Hawaii, is limited. This has some implications on the identity of this species (see discussion). Crossland (1937, as *crosslandi*) mentioned the presence of *nubilosa* in the Red Sea, with no description: his observation should not be taken for granted (note that, in any case, well-supported records of *nubilosa* are known from the Red Sea).

Kenny (1960) also mentioned the presence of *nubilosa* from Queensland (in Moreton Bay, Dunwich, Goat Island, Redland Bay, Curtis Island, Gladstone), but no description was provided and his identification remains uncertain. Colin and Arneson (1995) photographed an animal from Mactan Island, Cebu, Philippines, which they identified as *Sebadoris nubilosa*: this specimen may be part of *nubilosa*, but the picture does not show all the characters necessary to identify *nubilosa* (especially the long conical papillae on the notum) and this individual could also be part of *Sebadoris fragilis*.

Finally, several records of *nubilosa* or *Sebadoris* in the literature are erroneous. The specimen called *Sebadoris* sp. by Debelius (1996), the specimen called *Sebadoris* sp. by Ono (1999), and the specimen called *Discodoris nubilosa* by Allan (1947) are part of *raripilosa* (see this species). White

(1951:253, fig. 19) mentioned what was "probably a young of *Thordisa crosslandi*" from the Red Sea (a specimen that could be at the NHM, as B.M. No. 232). However, the radular formula −58 × (17-0-17)− suggests that she dissected a *Paradoris* specimen, although she found an unarmed labial cuticle.

WWW.— A picture of a specimen of *nubilosa* was posted on Mike Miller's Slug Site by Terry Gosliner. This specimen has the typically long, conical papillae on the dorsal notum. It was collected during a night dive from Mactan Island, Cebu, Philippines. Unfortunately, the specimen was lost and could not be dissected for the present study. The 60 mm (alive) long specimen photographed by Jun Imamoto from Miura Peninsula, Sagami Bay, on November 11, 2001, in the intertidal zone, and posted on his website as a *lilacina*, could be part of *nubilosa*, but this is highly hypothetical.

OCCURENCE.— The literature and museum collections (present study) suggest that *nubilosa* is regularly found in the Indian Ocean and in French Polynesia. However, *nubilosa* does not seem to be common everywhere else: six specimens known from Hawaii (Kay and Young 1969; present study); four from Heron Island, Queensland (Marshall and Willan 1999); one from Indonesia (type of *gigantea*); one from the Philippines (see the **WWW** section above). Colin and Arneson (1995) wrote that *nubilosa* was relatively common on seagrass beds in Mactan Island, Cebu, Philippines. Regardless of the fact that this identification still needs to be verified, it seems to concern a localized commonness of this species. Several hypotheses may explain the pattern of distribution of *nubilosa*: 1) it is truly rare in all the regions where it has not been found; 2) it is not rare but it is not frequently encountered since divers do not spend so much time on sea grass flats, despite its large adult size (see habitat below); 3) there is not one widespread species, but rather several species with smaller ranges of distribution range (e.g., one species in the Indian Ocean and western Pacific; another species in French Polynesia and Hawaii; see discussion).

HABITAT.— Mixed sand and rubble, grass flats (CASIZ 070352), under rocks (Eliot 1903), on coral substrates (Edmunds 1971; Soliman 1980; Marshall and Willan 1999; CASIZ 071727), on sponges among Cymodocea (Edmunds 1971), possibly on seagrass beds (Colin and Arneson 1995). Kay and Young (1969) mentioned that *nubilosa* is "apparently a deep-water species which is occasionally found in shallow water." Finally, according to Gosliner (Mike Miller's Slug Site), the coloration of *nubilosa* makes it "very cryptic on sand or coral rubble bottoms." Finally, several authors (e.g., Kay and Young 1969; Soliman 1980) mentioned that *nubilosa* was able to swim very well.

LITERATURE.— Several authors provided some information about the color of the dorsal notum (e.g., Pease 1871; Kay and Young 1969; Edmunds 1971; Soliman 1980; Marshall and Willan 1999). Valdés's (2002) re-description of the color of *nubilosa* was based on a picture of an animal from the Seychelles (no catalogue number provided) that was misidentified as *nubilosa* and that is actually part of *fragilis* (see this species): his re-description of the anatomy of *nubilosa* was based on another individual (CASIZ 071727) that is part of *nubilosa* but for which the color of the live animal is unknown. Several authors published some information about the internal anatomy of *nubilosa* (Eliot 1903, as *crosslandi*; Pruvot-Fol 1954b, as *ellioti*; Marcus and Marcus 1960a, as *crosslandi*; Kay and Young 1969, as *nubilosa*; Edmunds 1971, as *nubilosa*; Valdés 2002, as *nubilosa*). So far, the most detailed and best anatomical description (including the early embryological development) was published by Soliman (1980), based on specimens from the Red Sea. However, character variation was never addressed, except for some comments by Soliman (1980); three original descriptions and several re-descriptions were based on a single specimen or provided a unique synthetic drawing of the reproductive system, which prevented authors from representing variation (e.g., Edmunds 1971).

REMARKS ON THE ORIGINAL DESCRIPTION (*nubilosa*, Fig. 142A).— Although the original description is brief, it provides the diagnostic feature of *nubilosa*: the presence of soft, long, conical papillae of unequal size on the dorsal notum. It also provides some important characters of the external morphology, such as the presence of digitiform oral tentacles and a bilabiate anterior foot with a notched superior lip. The papillae as well as the color of the living animal are precisely represented on a color drawing. No internal organs were described.

Remarks on the original description (*crosslandi*, Figs. 142B-D).— The original description of *crosslandi* is largely complete. It provides precise information on the color of live animals, the external morphology, and some internal organs as well. The largest, preserved specimen was 125 mm in length. The dorsal notum is "sandy with blotches of brown irregularly bordered with black." The ventral surface is whitish with numerous brownish spots and a brownish border." The dorsal notum is covered with "thick-set pointed papillae, some of which are developed into distinct filaments at their extremities. The general texture is soft [the dorsal papillae lack spicules]." The branchial opening is not stellate. There are six tripinnate branchial plumes. The foot is bilabiate, with a notched upper lip. The oral tentacles are digitiform, but Eliot does not indicate whether they were grooved or not. On the labial cuticle, Eliot observed an "irregular collection of rods" that could "hardly be described as plates since the outline is ill-defined and the texture loose." The same phenomenon was observed in some specimens dissected here (see below). The radular formula is 45/55 × (80-0-80). The teeth are simply hamate, with no denticles. The description of the reproductive system is limited to the penis: "long, twisted spirally, and provided with two rows of tubercles."

Remarks on the original description (*gigantea*, Figs. 143A-C).— The animal measured 145 mm in length. The color of the dorsal notum was grey-brown with darker blotches of various sizes. Also, more importantly, the "very delicate," "not rigid" dorsal notum is covered with conical papillae (up to 2 mm long). Bergh described the basic discodorid features, such as an anterior bilabiate foot with a notched upper lip, and digitiform oral tentacles. Apparently, Bergh did not observe real jaws, which could be due to the fact that jaws are not always conspicuous in *nubilosa* (see below). The number of teeth provided by Bergh (from 150 to 200) likely is per row, and the radular formula thus is 70 × (75/100-0-75/100). Teeth are simply hamate, with no denticles. Bergh's description of the reproductive system is specifically interesting: the penis measures 7 mm long (Bergh, 1905, plate XV, fig. 15); the presence of humps on one side of the penis strongly sug-

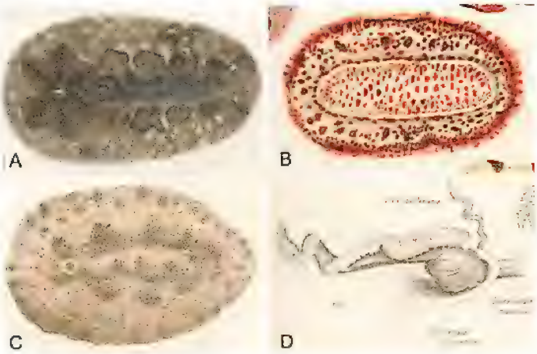

FIGURE 142. *Sebadoris nubilosa*, illustrations from original descriptions (except C). A. Dorsal color, original description of *Doris nubilosa* (Pease 1871: plate 6).— B. Ventral color, original description of *Thordisa crosslandi* (Eliot 1903: plate XXXII, fig. 3).— C. Dorsal color, description of *Thordisa crosslandi* (Eliot 1910a, plate 25, fig. 1).— D. Penis, original description of *Thordisa crosslandi* (Eliot 1903, plate XXXIII, fig. 6).

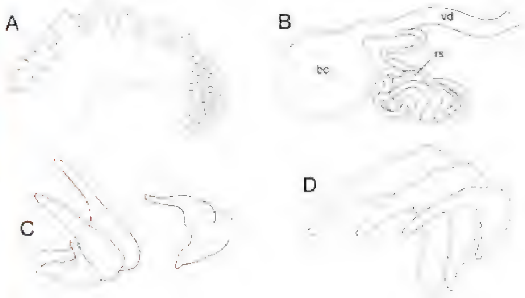

FIGURE 143. *Sebadoris nubilosa*, illustrations from original descriptions. A. Penis, *Diaulula gigantea*, after Bergh (1905: plate XV, fig. 15).— B. Spermatic pouches, *Diaulula gigantea*, after Bergh (1905: plate XV, fig. 16).— C. Outermost teeth (three left teeth) and innermost tooth (right tooth), *Diaulula gigantea*, after Bergh (1905: plate XV, figs 11 and 13).— D. Outermost teeth, *Argus indicus*, after O'Donoghue (1932: fig. 6D).

gests that Bergh observed specimens of *nubilosa*, although it is unclear whether those humps are placed on two rows. Finally, Bergh drew a receptaculum seminis covered (in a peculiar way) by the deferent duct, which was found in a few of the specimens of *nubilosa* dissected here.

Remarks on the original description (*indicus*, Fig. 143D).— In addition to the original description, some comments that Satyamurti (1952) wrote on the type specimen of *indicus* are also considered. The preserved specimen measured 140/8 mm. The color of the preserved specimen was "dirty grey mottled with dark grey and black, much as in *Discodoris fragilis*." The ventral surface of the notum was "yellowish grey with irregular brown-black patches which become confluent not only near the body but also at the margin." The foot was "yellow grey, with irregularly distributed almost circular brown-black spots." Satyamurti, who indicated that the "preserved specimen still [retained] a considerable part of its original color markings" described the color of the dorsal notum as "dirty grayish brown (…), mottled with large, dark grey and blackish patches." The mantle contains no spicules. The dorsal notum is covered with "small circular tubercles, each with a small blunt tip." Satyamurti described those tubercles as "small, close-set, rounded papillae, with somewhat pointed tips." There are six quadripinnate branchial plumes. The foot is bilabiate, with a notched upper lip. The oral tentacles are digitiform, but O'Donoghue does not specify whether they are grooved or not. O'Donoghue described a labial cuticle covered with chitin, which could mean that he did not see any rodlets or jaw plates. Nonetheless, O'Donohue considers that *indicus* has a labial armature. One specimen with a smooth labial cuticle (CASIZ 074202) was also found here. However, given that O'Donoghue did not take any SEM pictures, we cannot exclude that he overlooked some (inconspicuous) rodlets. The radular formula is 48 × (92-0-92). The teeth are simply hamate, with no denticles. O'Donoghue described the innermost tooth with a "triangular projection on its median side [and with] a small, curved, conical blade which is sometimes twisted at the end." The small triangular projection is commonly found in discodorids. The second feature is probably due to some artifact or natural individual variation. Unfortunately, the reproductive system was not described, neither by O'Donoghue nor by Satyamurti. The penial morphology remains unknown.

Description of new specimens (Figs. 144-153).— *Color*. None of the specimens dissected for the present study were photographed alive. However, according to Terry Gosliner (pers. com.), who collected some of those specimens, their color was similar to the illustrations published by Pease (1871) for *nubilosa* and Eliot (1903) for *crosslandi*: dorsal surface mottled with irregular brown blotches over a creamish-brown ground color. Some dorsal blotches are eye-like, with a whitish center surrounded by a darker circle. The ventral side of the body (foot and hyponotum) is creamish. The foot bears many brown spots, including large ones. In addition to spots, the hyponotum bears an irregular ring on its edge. Preserved animals can be homogeneously whitish (CASIZ 074202, CASIZ 074254) or still retain some fuzzy traces of spots and dots (CASIZ 071727, NMNH 576413, NMNH 576435).

External morphology. The body is oval. Its length equals less than twice its width. The largest specimen was 130/90 mm (NMNH 576413). The foot is rounded posteriorly and anteriorly. The width of the foot equals about one third or one half of the width of the dorsal notum (in preserved specimens). The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, not grooved. The dorsal notum bears soft, conical, pointed papillae. The latter are never branched and of unequal sizes. In large specimens, some preserved papillae measure up to 5 mm in length (NMNH 576413). Many small holes (diameter < 10 µm) and many small tufts of cilia were found on the surface of the papillae. No spicules could be seen on the surface of the notum, which is related to the fact that the notum seems to lack spicules, which is quite exceptional in discodorids. In a few specimens (CASIZ 071727; NMNH 576413), the dorsal notum consists of two layers: a thin layer of the mantle itself, and a thick muscular layer. In preserved spec-

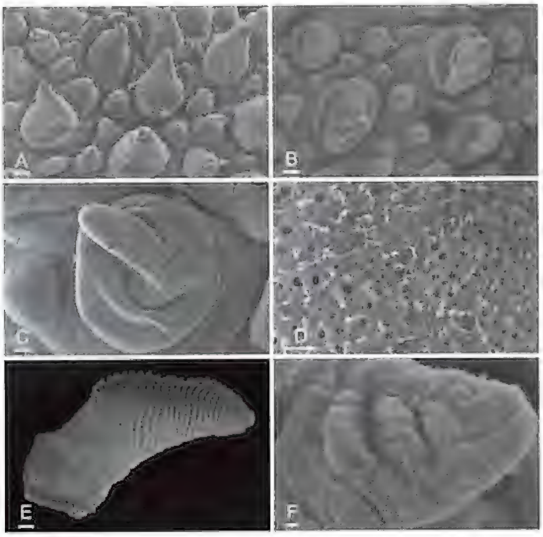

FIGURE 144. *Sebadoris nubilosa*, dorsal notum. A. Tubercles, CASIZ 074254, scale = 200 μm.— B. Tubercles, CASIZ 074254, scale = 200 μm.— C. Tubercles, CASIZ 074202, scale = 100 μm.— D. Dorsal notum, CASIZ 074202, scale = 20 μm.— E. Rhinophore, CASIZ 074254, scale = 300 μm.— F. Branchial plume, detail, CASIZ 074254, scale = 10 μm.

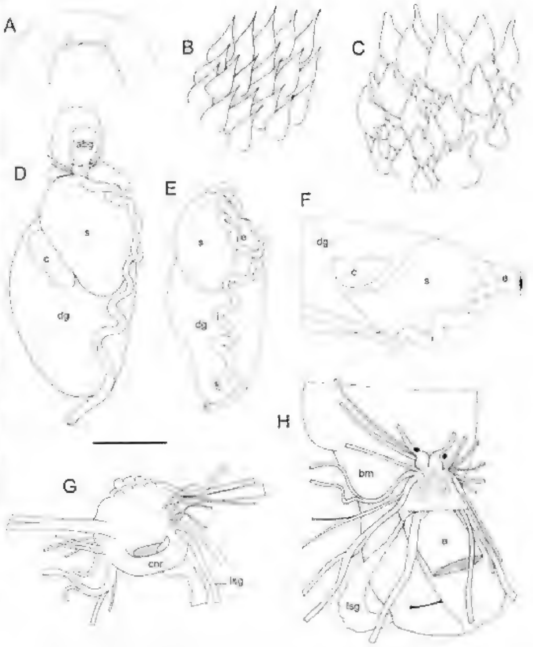

FIGURE 145. *Sebadoris nubilosa*. A. Anterior, ventral view, CASIZ 074254, scale = 20 mm.— B. Dorsal papillae, CASIZ 074254, scale = 4 mm.— C. Dorsal papillae, NMNH 576413, scale = 4.5 mm.— D. General anatomy, CASIZ 074254, scale = 12 mm.— E. Digestive system, lateral view, CASIZ 074254, scale = 14 mm.— F. Digestive system, lateral view, CASIZ 071727, scale = 9 mm.— G. Nervous system, posterior view, CASIZ 074254, scale = 2 mm.— H. Buccal mass and nervous system, CASIZ 074254, scale = 2 mm.

imens, the margins of the rhinophoral and branchial sheaths can be smooth or crenulate. The margin of the gill opening is not star-shaped with five lobes. There are six wide tetra- or tripinnate branchial plumes arranged in circle around the anus. The rhinophores have from 25 to 35 lamellae.

Digestive system. The stomach is large, free, on top of left, anterior digestive gland. A large caecum is located on the left posterior side of the stomach. The caecum is much larger than in other discodorid species studied here. The intestine is much longer than usual as well. It is highly convoluted (with several loops) from the stomach up to the anus. It is not strictly dorsal: it starts on the dorsal side of the digestive gland, then moves to the right side of the gland, reaches the bottom of the body cavity, and finally, gradually goes back to the dorsal side of the digestive gland. In most specimens, the labial cuticle is armed with a pair of jaw plates consisting of long rodlets. In most cases, the jaws can be seen under a dissecting scope, with no SEM. However, the labial cuticle is smooth in one specimen (CASIZ 074202), possibly two (CASIZ 070352). In another specimen (CASIZ 074254), no jaws could be seen under the dissecting scope, and just a few rows of rodlets were found with SEM. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. The number of teeth per row is quite high. Radular formulae are: 30 × (70-0-70) in a 40 mm long specimen (NMNH 576435 #2), 30 × (75-0-75) in a 60 mm long specimen (NMNH 576435 #1), 34 × (85-0-85) in a 65 mm long specimen (CASIZ 070352), 35 × (85-0-85) in a 70 mm long specimen (CASIZ 074202), 38 × (85-0-85) in an 80 mm long specimen (CASIZ 074254), 40 × (95-0-95) in a 110 mm long specimen (NMNH 576413 #2), 45 × (110-0-110) in a 130 mm long specimen (NMNH 576413 #1). The rachidian teeth are absent and the

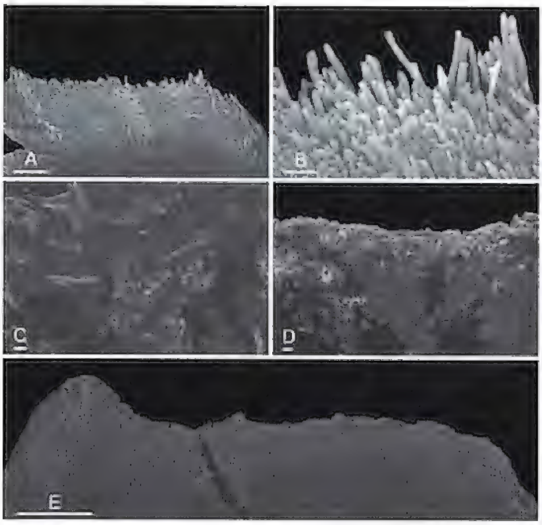

FIGURE 146. *Sebadoris nubilosa*, labial cuticle. A. Tubercles, USNM 576413 (#2), scale = 100 µm.— B. Tubercles, USNM 576413 (#2), scale = 20 µm.— C. Tubercles, CASIZ 074254, scale = 100 µm.— D. Dorsal notum, CASIZ 074254, scale = 10 µm.— E. Rhinophore, CASIZ 071727, scale = 100 µm.

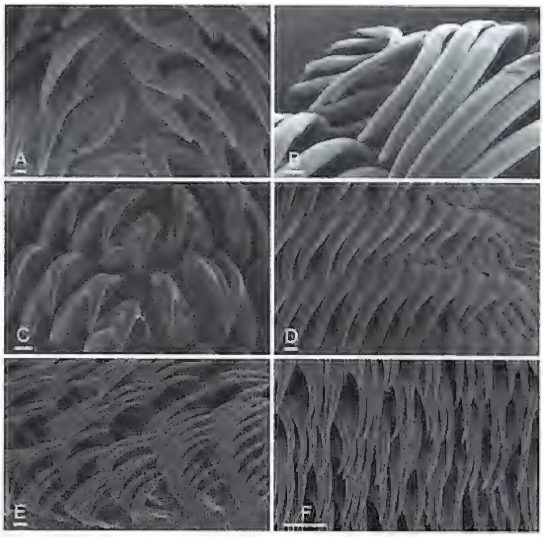

FIGURE 147. *Sebadoris nubilosa*, radula. A. Innermost teeth, CASIZ 070352, scale = 10 µm.— B. Outermost teeth, CASIZ 070352, scale = 10 µm.— C. Innermost teeth, CASIZ 074254, scale = 20 µm.— D. Outermost teeth, CASIZ 074254, scale = 20 µm.— E. Outermost teeth, CASIZ 074202, scale = 100 µm.— F. Median teeth, CASIZ 074202, scale = 30 µm.

rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the four or six innermost teeth of which the size increases gradually and the last four or six outermost ones of which the size decreases gradually. All teeth are hamate, including the outermost ones. The teeth bear no denticle.

Nervous system. The length of the circum-esophageal nerve ring ranges from one (in most specimens) to four (e.g., NMNH 576435 #2) times the width of the cerebro-pleural ganglia. The cerebral, pleural, and pedal ganglia are fused in a general nervous mass covered with large tubercles.

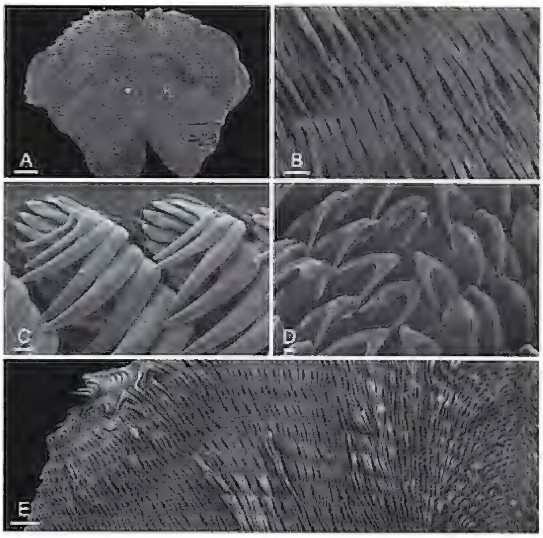

FIGURE 148. *Sebadoris nubilosa*, radula. A. USNM 576413 (#1), scale = 1 mm.— B. Median teeth, USNM 576413 (#1), scale = 100 µm.— C. Outermost teeth, USNM 576435 (#2), scale = 20 µm.— D. Innermost teeth, USNM 576413 (#1), scale = 20 µm.— E. Left rows, USNM 576413 (#1), scale = 300 µm.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla can be tightly or loosely convoluted. It can make several loops (e.g., CASIZ 074254) or be almost straight (CASIZ 070352). The division between male and female ducts (in the female gland mass) could not be seen by dissection. The prostate is divided in a proximal whitish part and a distal yellowish part. In one specimen (CASIZ 070352), this distinc-

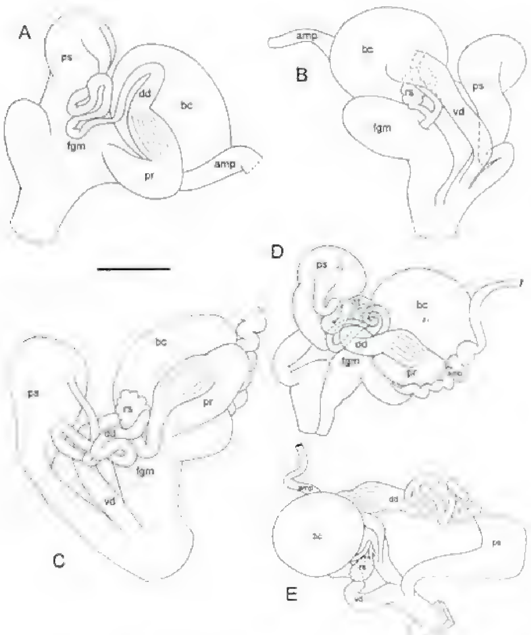

FIGURE 149. *Sebadoris nubilosa*, reproductive system. A. CASIZ 070352, scale = 1.3 mm.— B. CASIZ 070352, scale = 1.5 mm.— C. CASIZ 074202, scale = 1.5 mm.— D. CASIZ 074254, scale = 3 mm.— E. Organs separated from one another, CASIZ 074254, scale = 3 mm.

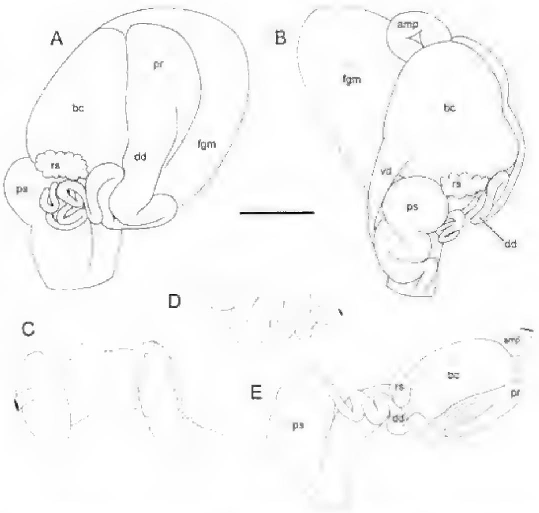

FIGURE 150. *Sebadoris nubilosa*, reproductive system. A. NMNH 576413 (#1), scale = 7 mm.— B. NMNH 576413 (#1), scale = 7.8 mm.— C. Penis, NMNH 576413 (#1), scale = 3.3 mm.— D. Ampulla, NMNH 576413 (#1), scale = 10 mm.— E. NMNH 576435 (#1), scale = 2.2 mm.

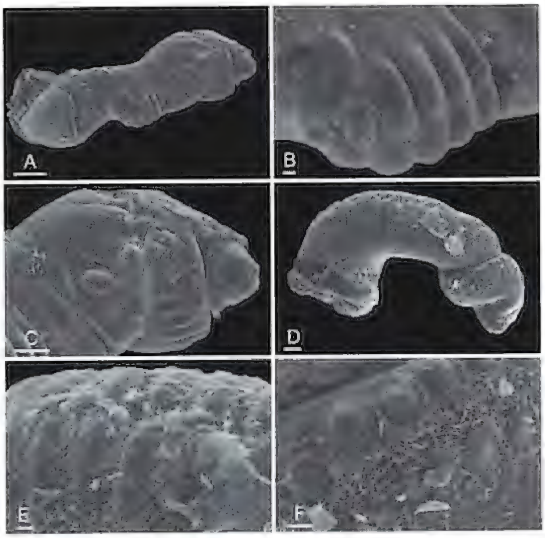

FIGURE 151. *Sebadoris nubilosa*, penis. A. CASIZ 074202, scale = 200 µm.— B. CASIZ 074202, scale = 20 µm.— C. CASIZ 074202, scale = 100 µm.— D. CASIZ 070352, scale = 100 µm.— E. CASIZ 070352, scale = 20 µm.— F. CASIZ 070352, scale = 30 µm.

tion could not be observed. The deferent duct is convoluted, with many tight loops or only a few loose loops. The proximal end of the deferent duct is wide, internally folded in two specimens (CASIZ 074254; CASIZ 070352). The ampulla and the deferent duct can be highly convoluted, even if the female gland mass is poorly developed (e.g., NMNH 576435). The deferent duct ends in a distinct penis, which is coiled in most cases. It bears small humps on its surface. The shape and the position of those humps vary among specimens. In most specimens, there are two longitudinal rows of humps. In one specimen, it seems that the conical humps alternated along one longitudinal line (NMNH 576413 #1). In the two smallest specimens (NMNH 576435 #1 and #2), the penis is a smooth, uncoiled papilla. The reproductive system of the smallest specimen (NMNH 576435 #2) was immature (the female gland mass was absent), which suggests that the humps on the surface of the penis do not appear right at the beginning of the penial development. The vaginal duct is almost straight. The deferent duct and the vaginal duct join and form a vestibule that may or may not remain separate from the female duct (it depends on which side we look at −CASIZ

070352). The fertilization duct is short and almost not convoluted. The connection between the fertilization duct and the female gland mass is marked by a clear duct. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is underneath the vaginal duct. The bursa copulatrix is up to seven times larger than the receptaculum seminis. The bursa copulatrix is spherical-ovate and smooth, whereas the receptaculum seminis is elongated, with grape-like protuberances on its surface. The receptaculum seminis can be covered by the deferent duct.

Diagnostic features.— The presence of long, conical papillae on the dorsal notum is diagnostic of nubilosa. Long conical papillae are also found in other taxa such as Thordisa and Asteronotus, but the dorsal notum of nubilosa is entirely covered with tightly adjacent papillae, which is unique. The color, also, should help. However, one should be careful because a grayish dorsal background with darker blotches can be easily confused with other discodorids, especially Sebadoris fragilis. A good diagnostic anatomical character is the penis, bearing two longitudinal rows of humps (although the latter can be absent in small specimens with an immature reproductive system. The presence of a receptaculum seminis with a grape-like surface, although found in other species, may also help for identification purposes.

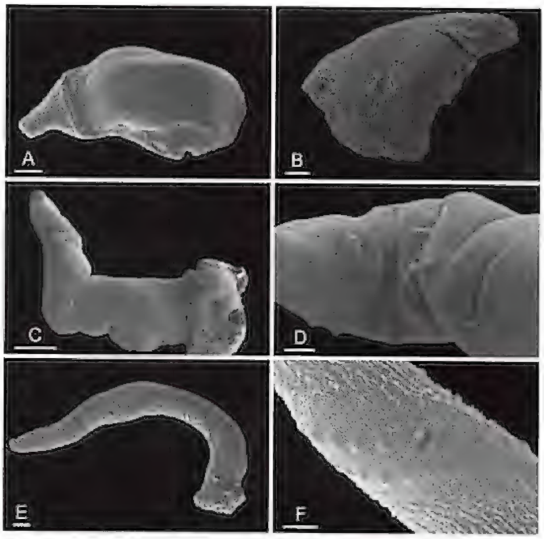

Figure 152. *Sebadoris nubilosa*, penis. A. USNM 576435 (#2), scale = 100 µm.— B. USNM 576435 (#1), scale = 100 µm.— C. USNM 576413 (#1), scale = 1 mm.— D. CASIZ 070352, scale = 200 µm.— E. CASIZ 074254, scale = 200 µm.— F. CASIZ 074254, scale = 100 µm.

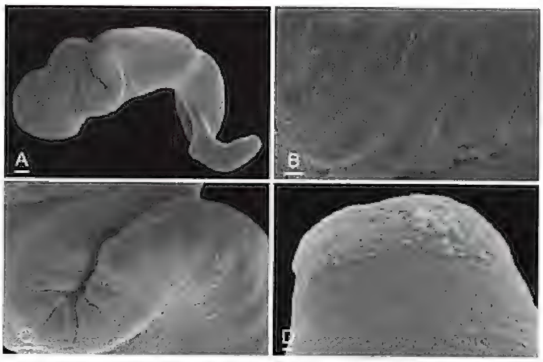

Figure 153. *Sebadoris nubilosa*, penis, USNM 576413 (#2). A. Scale = 300 µm.— B. Scale = 100 µm.— C. Scale = 200 µm.— D. Scale = 20 µm.

Infra-specific character variation— Present observations are fully compatible with the anatomical descriptions available in the literature. The animals are large: up to 110 mm preserved (Marcus and Marcus 1960a), 140 mm alive (Edmunds 1971), 200 mm alive (Kay and Young 1969), 250 mm alive (Soliman 1980). Observing and describing the labial cuticle was a problem for several workers. Edmunds wrote that the labial cuticle (of a 120 mm long animal) was "almost smooth," which suggests that he probably did not know whether it was smooth or armed. According to Kay and Young (1969:181), "the jaws have no hooks, but slightly raised granulations, appearing as dorso-ventral ridges, are present." Marcus and Marcus (1960a) observed two jaw plates in large specimens, but did not find them in small animals; Soliman (1980) seem to have found "small but well-defined" jaw plates in his material from the Red Sea. In summary, jaws are present in most specimens, although they can only be observed easily through SEM. However, jaws can also be reduced to a few rows of inconspicuous rodlets, and occasionally be absent. One could not exclude that a reduced jaw could be due to an artifact of preparation (e.g., how long the labial cuticle remains in NaOH), but it is difficult to explain why it would have happened to several workers independently, and just with that particular species. Radular formulae available in the literature are: 45 × (97-0-97) in a 110 mm long specimen, preserved (Marcus and Marcus 1960a), 45 × (105-0-105) in a 120 mm long specimen, alive (Soliman 1980), 50 × (105-0-105) in a 120 mm long specimen, preserved (Edmunds 1971), 52 × (120-0-120) in a 200 mm long specimen, alive (Kay and Young 1969), 55 × (116-0-116) in a 190 mm long specimen, alive (Soliman 1980), 65 × (130-0-130) in a 250 mm long specimen, alive (Soliman 1980). In summary, the number of rows ranges from 40 (present study) to 65 (Soliman 1980), and the number of teeth per half-row ranges from 70 (present study) to 130 (Soliman 1980). The two longitudinal rows of humps were described carefully and illustrated by several authors: Pruvot-Fol (1954b:17, fig. 20a, as *ellioti*), Marcus and Marcus (1960a:903, figs 53-54), Edmunds (1971: fig. 4B) who calls them "thorn-like processes," and Soliman (1980:233, figs 6-7). Pruvot-Fol (1954b:17, fig. 20b), Kay and Young (1969: fig. 6B), Edmunds (1971: fig. 4B), and Soliman (1980:233, figs 6-7) observed a receptaculum with a grape-like surface.

DISCUSSION.— The first question that needs to be addressed here is: are there two distinct species (*crosslandi* and *nubilosa*), as accepted by several authors (Marcus and Marcus 1960a; Soliman 1980) or just one (*nubilosa*), as first proposed by Kay and Young (1969). Bergh (1905) did not compare *gigantea* with any other species, including *crosslandi*, described in 1903 by Eliot. The synonymy between *crosslandi* (type locality Zanzibar) and *gigantea* (type locality Indonesia) was demonstrated by Eliot (1906b). There is not much to add to Eliot's argument, except that contrary to what Eliot was thinking, *Phialodoris podotria* Bergh refers to a different species (because its penis is different from that of *crosslandi*, i.e., *nubilosa*). This synonymy has never been rejected. Later on, another species, *Argus indicus*, was described by O'Donoghue (1932) from the Gulf of Manaar. O'Donoghue did not compare *indicus* with *crosslandi* or *gigantea*. The synonymy between *indicus* and *crosslandi* was proposed by Satyamurti (1952), based on Winckworth's idea. This synonymy has not been mentioned since then: authors have not taken the Gulf of Manaar into account for the distribution of *crosslandi*; Dorgan et al. (2002) suggested that *indicus* should be part of *nubilosa*, without citing Satyamurti. This synonymy is likely correct, although we ignore the penial morphology because O'Donoghue did not describe the reproductive system: the absence of spicules in the dorsal notum and the presence of "small tubercles with a small blunt tip" (O'Donoghue 1932), also described as "small, close-set, rounded papillae, with somewhat pointed tips" (Satyamurti 1952) suggest that *indicus* was part of *nubilosa* (or, at least *crosslandi*).

Eliot was aware of the affinities between *nubilosa* and *crosslandi*. In 1910, he wrote that: "the *Doris nubilosa* of Pease is perhaps the same as this form [*crosslandi*] but the identity is hardly demonstrable." (Eliot 1910a:421) Since then, most authors (Kay and Young 1969; Edmunds 1971; Kay 1979; Marshall and Willan 2001; Valdés 2002) have accepted a synonymy of *crosslandi* with *nubilosa*. Marcus and Marcus (1960a, 1970) and Soliman (1980), however, thought that there were two distinct species. The infra-specific variation of several key features (e.g., labial cuticle, penial shape) addressed in the present study helps solve this issue. All the differences between *nubilosa* and *crosslandi* listed by Soliman (1980) can be explained through individual variation: absence/presence of distinct jaw plates; radular teeth of different size; size of the vaginal duct; shape of the receptaculum seminis. The variation observed among the specimens dissected here was not correlated to geographic distribution. For instance, no geographic pattern could be found for the penial morphology.

Another question that must be addressed is whether or not *nubilosa* could be confused with other species. Several specimens identified as *nubilosa* in museum collections are part of *Sebadoris fragilis*. Also, several authors mentioned a close resemblance between *fragilis* and *nubilosa*

(O'Donoghue 1932, as *indicus*; Marshall and Willan 2001). Confusion is quite possible for small, preserved specimens. Both species share several features not found in other species, such as a body wall with two layers (an external, thin skin, and a thick, muscular tissue) and a long, convoluted intestine. However, both species differ for at least two important features: 1) the notum of *fragilis* is rich in spicules (and the tubercles are not soft), whereas the notum of *nubilosa* is spicule-free (and the tubercles are soft); 2) the penis of *fragilis* is smooth and conical, whereas the penis of *nubilosa* bears two longitudinal rows of humps. In addition, note a few potentially interesting characters: 1) the foot and the hyponotum of *nubilosa* (see, e.g., Kay and Young 1969:180, fig. 7B; Soliman 1980:228, fig. 1C; Marshall and Willan 2001:225, fig. 150) bear some distinct, dark blotches on a whitish background, whereas the foot and the hyponotum of *fragilis* bears multiple dots and spots that give it a fuzzy appearance; 2) specimens of *fragilis* tend to be smaller (up to 150 mm) than *nubilosa* (up to 200 mm); 3) the radula of *fragilis* tends to have fewer teeth per half-row (exceptionally, up to 90/100) than in *nubilosa* (up to 130). Clearly, the last two features must be used with caution because the range of number of teeth per half-row and the size range overlap in both species.

A few interesting misidentifications from the literature are mentioned here. Pruvot-Fol's (1954b) specimen of *Austrodoris ellioti* (Alder and Hancock) is part of *nubilosa* because of the *nubilosa*-type penis and also the receptaculum seminis with small grape-shaped protuberances on its surface; Pruvot-Fol's identification (which she recognized was uncertain) was largely arbitrary. Several specimens identified as *Sebadoris* or *Discodoris nubilosa* are all part of *Asteronotus raripilosa* (see this species): specimens identified as *Sebadoris* sp. by Debelius (1996) and Ono (1999); specimens identified as *Sebadoris* sp. cf. *nubilosa* by Ono (2004); and a specimen identified as *Discodoris nubilosa* by Allan (1947). However, *raripilosa* and *nubilosa* are easily recognized thanks to the branched papillae of *raripilosa*. The internal anatomy is extremely different as well (see *raripilosa*).

SUPRA-SPECIFIC RELATIONSHIPS.— In total, *nubilosa* was classified (under various species epithets) in eight different genera: it was originally described in four distinct genera (as *Doris nubilosa*, *Thordisa crosslandi*, *Diaulula gigantea*, and *Argus indicus*); it was re-allocated to three different genera (*Discodoris*, *Archidoris*, and *Sebadoris* −the latter being monotypic); and, finally, it was misidentified as *Austrodoris ellioti*. The generic affinities of *nubilosa* are clearly not obvious.

Pease placed *nubilosa* in *Doris* because discodorid genera (such as *Discodoris*, *Anisodoris*, and *Peltodoris*) had not been named at that time.

Eliot rightly wrote that it was "extremely difficult to determine the true affinities of [*crosslandi*]." He classified it in *Thordisa* because of the soft pointed papillae. However, the papillae of *crosslandi* differ from that of *Thordisa* (in *Thordisa*, papillae are not soft as in *nubilosa* and also scattered, whereas they are densely cover the entire dorsal notum in *nubilosa*); and, also, *crosslandi* lacks one important synapomorphy of *Thordisa*, i.e., the pectinate outermost teeth. Eliot did not think that the presence of pectinate outermost teeth was a valid generic characteristic of *Thordisa*, however. Eliot (1903, 1906b) wrote that *crosslandi* had a similar penis to that of *Phialodoris*. Bergh's drawing of the penis of *Phialodoris podotria* is different from that of *nubilosa*, and *nubilosa* does not belong to *Phialodoris*, nor is a senior synonym of *podotria*.

Bergh (1905) was not sure that *gigantea* should be classified in *Diaulula*, which he clearly emphasized by adding a question mark between *Diaulula* and *gigantea* in the original description. Certainly, the lack of jaws (traditionally, *Diaulula* species lack jaws) influenced his choice (although Bergh may have overlooked some rodlets). Eliot (1906b) thought that the distinction between *Diaulula* and *Thordisa* was "perhaps not very clear" and preferred to leave *crosslandi* (which he regarded as the valid species name for *Diaulula gigantea*) in *Thordisa*, rather than reallocating it to *Diaulula*.

O'Donoghue placed *indicus* in *Argus*, i.e., *Platydoris*, for unspecified reasons. He simply commented on the fact that the presence (*indicus*) *versus* absence (*Argus*) of an armed labial cuticle was not a "good generic character." He actually compared *indicus* with *fragilis* in detail (and, rightly regarded them as two distinct species), but did not explain why he did not classify *indicus* in *Discodoris*.

Finally, Pruvot-Fol (1947) thought that *nubilosa* should be classified in *Discodoris*, but did not add any new data.

The classification of *nubilosa* is a good example of what people actually do when they have no idea of the generic-level relationships of a given species: they place it in an arbitrary genus, or create a monotypic genus for it. These solutions are not satisfactory, because they tend to hide the fact that we ignore the generic level relationships (Dayrat and Gosliner 2005).

In any case, a phylogenetic test of the relationships of *nubilosa* suggests that it is closely related to *Sebadoris fragilis*, in a clade called *Sebadoris* (given that *nubilosa* is the type species of *Sebadoris*) which might explain why they have been confused so often. The Linnaean binomial is *Sebadoris nubilosa*, which also is a possible name under the *ICPN*.

Sebadoris fragilis **(Alder & Hancock, 1864) new combination**

Figures 154-188.

Doris (*Dendrodoris*) *granulata* Ehrenberg, 1831: no page number.
Pterodoris granulata.— Bergh, 1877b:60-61.
Discodoris granulata.— Bergh, 1878a: XXVII.— O'Donoghue, 1929:721.
Doris maculosa.— Quoy and Gaimard, 1832:249-250, plate 16, figs 3-5 [may or may not be *maculosa* Cuvier, 1804, regarded here as a *nomen dubium*; this specimen became the type of *Discodoris vanikoro* Pruvot-Fol, 1934].
Doris sordida Quoy and Gaimard, 1832:266, plate 19: figs 12-13 [permanently invalid name, preoccupied by *Doris sordida* Rüppell and Leuckart, 1831, replaced before 1961 by *Doris sordidata* Abraham, 1877].
Platydoris ? *sordida*.— Bergh, 1878a: XXXVI.
Discodoris sordida.— Pruvot-Fol, 1935:220.
Doris fragilis Alder and Hancock, 1864:118-119, plate XXVIII, figs 7-8.
Discodoris fragilis.— Bergh, 1877a:519.— Bergh, 1878a: XXVII.— Bergh, 1884a:93.— Eliot, 1900:517-518.— Eliot, 1906b:652.— Eliot, 1906c:1004.— Eliot, 1909a:87-89.— Eliot, 1910a:422-423.— Edmunds, 1971:347-349, figs 3, 4C.— Edmunds, 1972:70-73.— Rao and Kumary, 1974:689-698, figs 1-3, plate I, figs. A-D.— Orr, 1981:47.— Tan et al., 1987:77, 83, fig. 13.— Yonow and Hayward, 1991:17, figs 10A-B.— Wells and Bryce, 1993:99, fig. 118.— Marshall and Willan, 1999:72-73, 218, fig. 123.— Coleman, 2001:56, unnumbered figure.— Yonow, 2008:150-151, three unnumbered figures.
Doris sordidata Abraham, 1877:206 [in replacement of *Doris sordida* Quoy and Gaimard, 1832]. **New synonym.**
Argus sordidata.— O'Donoghue, 1929:729.
Discodoris sordidata.— Pruvot-Fol, 1934:67-68, fig. 25.
Discodoris morphaea Bergh, 1877a:536-539, plate LX, figs 18-22, plate LXI, figs 1-5.— Bergh, 1884a:93-98, plate I, figs 19-22, plate II, figs 1-12, plate III, figs 13.— Pruvot-Fol, 1934:67.
Doris stragulata Abraham, 1877:203, 251-252, plate XXVIII, figs 7-8. **New synonym.**
Discodoris stragulata.— Bergh, 1878a: XXXVI.
Discodoris ? *stragulata*.— Bergh, 1880a:47.— Bergh, 1884a:93.
Discodoris concinniformis var. Bergh, 1888:809-811. **New synonym.**
Discodoris concinna.— Eliot, 1909a:89.— Vayssière, 1912, 21-23, figs 30-32.— Baba, 1933:276, fig. 2.— Baba, 1949:65, 151-152, fig. 79.— Baba, 1955:55, plate XVIII, figs 49-50.— Gohar and Soliman,

1967:198-212, figs 1-17.— Soliman, 1983:179-184, figs 1-6.— Willan and Coleman, 1984: p. 36, fig. 108.— Guangyu, 1986:124, plate II, fig. 7.— Coleman, 1989:23, unnumbered figure.— Soliman, 1991:260-261.— Wells and Bryce, 1993:99, fig. 117.— Dayrat and Gosliner, 2005:202, 218, 222 [not *concinna* Alder and Hancock, 1864]

Discodorididae concinna.— Dayrat and Gosliner, 2005:205 [not *concinna* Alder and Hancock, 1864].

Alloiodoris hedleyi O'Donoghue, 1924a:547-550, plate 27, figs 6-7, plate 30, figs 45-47. **New synonym.**

Discodoris rubra Bergh, 1905:104 [in part, not *Discodoris rubra* Bergh, 1905].

Discodoris vanikoro Pruvot-Fol, 1934:70-71. **New synonym.**

Peltodoris noumeae.— Risbec, 1956:8, plate III, figs 10-15, plate IV, figs 16-17, plate V, figs 23-24 [not *noumeae* Risbec, 1937].

Discodoris notiperda Risbec, 1956:15-16, plate IX, figs 43-49, plate X, figs 50-51. **New synonym.**

Discodoris sp. Coleman, 2001:56, unnumbered "AMPI 215" figure.

TYPE MATERIAL (*granulata*).— One holotype, by monotypy (ZMB no catalogue number). There is one label in the jar, and one label glued on the jar. Both labels say "*Discodoris granulata* Ehrenberg." Bergh, who examined this lot, likely re-labeled this *Doris* species as a *Discodoris*. However, both labels clearly indicate that the specimen is a type: specimen (or station) number 579, leg. Ehrenberg and Hemprich; a blue label, likely the oldest one, is not readable.

TYPE MATERIAL (*fragilis*).— A few (at least two) syntypes (NEWHM 2002.H2555, NEWHM 2002.H2575, and four slides 3/23/04, 3/23/06, 3/23/07, 3/23/32). Alder and Hancock mentioned two specimens in the original description of *fragilis*. The Hancock Museum, Newcastle, holds two jars that contain several pieces of notum of these two specimens. However, there might be more than two specimens. The former label of these jars indicated: "N°32, *Doris fragilis*, Madras, Sir Walter Elliot." One jar (NEWHM 2002.H2555) contains six pieces of dorsal notum, and an empty body wall (with the pedal sole and part of the dorsal notum); these pieces could be part of one, two, or even three different individuals. A piece of notum from this jar was mounted on a SEM stub. The other jar (NEWHM 2002.H2575) contains the body wall of one specimen (including the foot, an almost complete notum, and the digestive gland inside), measuring 70/45 mm, and a piece of dorsal notum of another individual that approximately measures 60/40 mm. Eliot (1906c) found four slides labeled as "*D. bellicosa* 32" in Walter Elliott's collection from eastern India, which Alder and Hancock (1864) used to name several new species. Eliot thought that these slides were part of the type material of *fragilis* because: 1) the syntypes of *fragilis* are numbered "32" and labeled "*D. fragilis*," and 2) Alder and Hancock wrote in the original description of *fragilis* that they originally regarded the two type specimens of *fragilis* as part of *D. bellicosa* Kelaart, 1859, the only species to which they compared *fragilis*. Eliot is probably right that the two slides labeled "*D. bellicosa* 32" are part of the type material of *fragilis*. These four slides include two radulae (3/23/04, 3/23/32) and two labial cuticles (3/23/06, 3/23/07).

TYPE MATERIAL (*stragulata*).— Holotype (NHM 1860.11.6.2), by monotypy: one specimen 70/40 mm preserved, leg. Cuming, [no collecting date].

TYPE MATERIAL (*morphaea*).— Holotype (ZMUC GAS-2130), by monotypy: one specimen 55/30 mm preserved, leg. Semper, November 1863.

TYPE MATERIAL (*sordidata*).— Holotype (MNHN, no catalogue number) by monotypy: one specimen 60/35 mm preserved, [collected by Quoy and Gaimard, aboard *l'Astrolabe*].

TYPE MATERIAL (*rubra*).— One paralectotype (ZMA 3.05.148): one specimen 75/35 mm preserved, leg. Siboga Expedition, 28 August 1899. The type material of *rubra*, deposited at the Zoölogisch Museum, Amsterdam, included two syntypes, one of which is part of *fragilis* (ZMA 3.05.148). Fortunately, Bergh distinguished the two specimens in his original description, largely based on the specimen that is not part of *fragilis*. In order to solve this nomenclatural problem, the syntype (ZMA 3.05.147) that is not part of *fragilis* is designated as the lectotype of *rubra*, and the other as a paralectotype. The paralectotype of *rubra* is not the name-bearer of *rubra*, although it is still part of the type material of *rubra*. Therefore, *Discodoris rubra* Bergh, 1905 is not a synonym of *fragilis*.

Type material (*hedleyi*).— Two syntypes (NHM 1922.925.18-19): two specimens 43/25 [very retracted] and >40/30 [cut in pieces] mm preserved, leg. E. Dakin and C. H. O'Donoghue, [collected during the Percy Sladen Trust Expeditions, from 1913 to 1915, see Dakin (1919)]. A radula, extracted from one of the two syntypes, is preserved on a slide (NHM, 1923.3.27.9). In addition, the NHM holds a co-type (NHM 1953.6.30.310), from the same locality, which is not part of the type material: one specimen 24/11 mm preserved, C. H. O'Donoghue, [no collecting date]. This co-type may be the small specimen mentioned in the original description, in addition to the two large specimens; however, it may not be part of the same species.

Type material (*vanikoro*).— Holotype (MNHN, no catalogue number), by monotypy: one specimen 75/55 mm preserved, leg. Quoy and Gaimard, [collected by Quoy and Gaimard, most likely in February, 1828]. The jar includes two labels. The oldest one, probably from the first half of the 20th century, reads: "*Discodoris Vanikoro*, Mrs Quoy et Gaimard, 1829." The other label, probably from the 1990s, reads: "*Discodoris* sp. (dét. Quoy et Gaimard), Vanikoro, coll. Quoy et Gaimard (entrée 1829)." Because the genus name *Discodoris* was created in 1877, Quoy and Gaimard could not identify ('*dét*' = determined, identified) this specimen as a *Discodoris*. However, Pruvot-Fol created the new name *Discodoris Vanikoro* [with a capital letter "V" exactly like on the label] for a specimen identified and described as *Doris maculosa* by Quoy and Gaimard (1832:249-250, plate 16, figs 3-5). Therefore, Pruvot-Fol probably just added a label with the new name *Discodoris Vanikoro* and removed the label with the original identification as *Doris maculosa*. Therefore, the specimen held by the MNHN and labeled "*Discodoris Vanikoro*" is most likely the holotype, by monotypy, of *Discodoris vanikoro*. Pruvot-Fol (1934) created the name *Discodoris vanikoro* as a *nomen novum*. However, this name was not a *nomen novum* in the strict sense. Indeed, it was not a new replacement name and the name-bearing type of *Discodoris vanikoro* is distinct from the (lost) name-bearing type material of *Doris maculosa* Cuvier, 1804. The case of *Doris maculosa* Cuvier, 1804, which regarded here as a *nomen dubium*, is discussed separately (see this species).

Type material (*notiperda*).— One lectotype (MNHN, no catalogue number), designated here: one specimen 55/30 (R^te^ 912, E. 34.239) mm preserved, leg. J. Risbec, [no collecting date]. Seven paralectotypes (MNHN, no catalogue numbers), designated here: seven specimens 75/50 (R^{te} 912, E. 34.237), 70/50 (R^{te} 912, E. 34.238), 60/40 (R^{te} 912, E. 34.236), 50/35 (R^{te} 196, E. 34.256), 40/30 (R^{te} 912, E. 34.240), 35/20 (R^{te} 196, E. 34.255), and 32/22 (R^{te} 196, E. 34.254) mm preserved, leg. J. Risbec, [no collecting date]. The numbers between parentheses refer to the numbers assigned by Risbec to every specimen: "R^{te}" probably means "récolte," i.e., field station, and "E." probably means "examplaire," i.e., "specimen number." Also, in the original description, Risbec mentioned an additional syntype, collected from Cua Be (R^{te} 150, E. 34.257); this specimen could not be found, and is probably lost. The reason to designate a single name-bearing type is that the specimen E. 34.254 (here a paralectotype) is probably not part of the same entity because it actually looks like a *Platydoris*. Also, the specimen dissected here was selected as the lectotype because the internal organs of the specimen entirely dissected by Risbec (E. 34.237) could not be found and are probably lost. Finally, note that the station numbers indicated on the labels do not correspond exactly to the station numbers in the original description: according to the original description, the three specimens E.34.254, E34.255, and E.34.256 were collected from the station R^{te} 150. However, Risbec also used this station number 'R^{te} 150' for the third locality, Cua Be; a mistake may have been introduced in the publication.

Type material (*concinniformis* var.).— Holotype (ZMB 43946), by monotypy: one specimen 65/48 mm preserved length.

Type locality (*granulata*).— Masssua [jar only], Red Sea.

Type locality (*fragilis*).— According to the label, the type locality is 'Madras.' However, according to the introduction of the original publication, the type locality of *fragilis* should be Waltair, eastern India. Walter Elliot, who collected these specimens studied by Alder and Hancock, described this locality as follows: "Waltair is a suburb of the town of Vizagapatam [i.e., Visakhapatnam], the capital of the province of the same name, one of the Northern Circas. The coast south of Vizagapatam is flat and sandy, with a heavy surf, which is unfavourable to the existence of naked Mollusks; but the whole of the coast of Vizagapatam is rocky, and sometimes precipitous, abounding in bays filled with rock and shingle, amongst which the delicate forms of the creatures you have been describing find shelter. Immediately to the north of Waltair is one of these bays, called Lawson's Bay, in which a large proportion of the specimens were found; but I employed men to search along a more extended line, both north and south of the bay. Most of the species were taken between tide-marks, and only one or two in deep water" (Alder and Hancock 1864:113). The type locality of *fragilis* certainly is eastern India, either Madras or Visakhapatnam.

Type locality (*stragulata*).— The type locality is unknown. It is not indicated in the original description. It is not indicated on the label of the type specimen either. We can reasonably hypothesize that the type locality of *stragulata* is somewhere in the tropical Indo-West Pacific.

Type locality (*morphaea*).— Ubay, Philippines.

Type locality (*sordidata*).— Ilots aux cerfs, île de France [Mauritius, Indian Ocean].

Type locality (*rubra*).— The type locality of *rubra* is the locality of the lectotype (see *rubra*). The locality of the paralectotype is the station 172 of the Siboga expedition: anchorage between Gisser Island and Ceram, Indonesia, 18 meters depth, 28 August 1899.

Type locality (*hedleyi*).— Abrolhos Island, [Western Australia].

Type locality (*vanikoro*).— Vanikoro, [western Pacific Ocean].

Type locality (*notiperda*).— Port Dayot, Nhatrang, [Nha Trang, Vietnam, South China Sea]. All type specimens were collected from Nha Trang, in three different localities: five specimens were collected from Port Dayot (Risbec's R^{te} 912), three specimens from the Nha Trang market (Risbec's R^{te} 196 according to the labels, and Risbec's R^{te} 150 according to the original description), one from Cua Be (according to the original description Risbec's R^{te} 150).

Type locality (*concinniformis* var.).— Ile aux Fouquets [not Phuket, Thailand, see Jensen, 1998], Mauritius, Indian Ocean. The label of the type material simply indicates Mauritius.

Type material condition (*granulata*).— The specimen is now homogeneously whitish. It was not dissected. It was opened carefully on the right ventral side, and it clearly has all internal diagnostic features of *fragilis*.

Type material condition (*fragilis*).— The pieces of notum held by the Hancock Museum are in poor condition. No internal organs remain, except for one digestive gland. The color of the dorsal surface of the notum (dark brown) is largely destroyed due to preservation. However, the pieces of notum are not uninformative: the color of the foot and the hyponotum is still distinguishable. The labial cuticles and the radulae on the slides (labeled as *D. bellicosa*) are in good condition, except for a dry radula on a slide (3/23/32).

Type material condition (*stragulata*).— Abraham did not dissect the holotype, but simply opened it on the right lateral side of the foot. All internal parts are still present in the body wall, including the radula. The reproductive system is poorly preserved.

Type material condition (*morphaea*).— Bergh dissected the holotype. In the jar, there currently are an empty body wall, the digestive gland, the intestine (detached from the digestive gland), the heart, the oral tube, and six branchial plumes. No slides could be found. The notum is poorly preserved.

Type material condition (*sordidata*).— The holotype was dissected by Pruvot-Fol (1934). The radula, illustrated by Pruvot-Fol, could not be found and is probably lost. The rest of the internal organs, partly dissected prior to the present study, are still present. The penial sheath, opened by by Pruvot-Fol, contains a small penis that may not be complete. A small tube contains some pieces of the oral tube and the buccal mass, but no jaw plates.

Type material condition (*rubra*).— Bergh dissected the paralectotype. The reproductive system and the buccal mass are missing and probably lost.

Type material condition (*hedleyi*).— O'Donoghue dissected both syntypes. In the jar, there are: a complete, greatly damaged body wall, and a few pieces of the notum and the digestive gland of a second specimen; a reproductive system (distal part missing) that could belong to any specimen. The radula slide is in good condition. The cotype, poorly preserved externally, is complete.

Type material condition (*vanikoro*).— The holotype was dissected by Pruvot-Fol. The buccal mass could not be found and is probably lost. The reproductive and digestive systems are still present.

Type material condition (*notiperda*).— Risbec dissected two paralectotypes: only the dorsal notum remains for the specimen E.34.237; all internal organs were left for the specimen E.34.236, including the buccal mass and the reproductive system. The condition of the specimen from Cua Be, probably lost, is unknown. The six other type specimens are entire and well preserved externally. The lectotype (E.34.239) is designated here.

Type material condition (*concinniformis* var.).— The specimen was dissected by Bergh, and only the external body wall (homogeneously whitish) remains in the jar.

Additional material dissected.— **Red Sea**, southern Egypt, 120 km South of Marsa Alam, February 2003, one specimen 35/23 mm preserved, leg. J. Hinterkircher, identified as *Discodoris fragilis* by J. Hinterkircher (CASIZ 170083); **Gulf of Aden**, Djibouti, [no collecting date but accession date 1904], two specimens 80/50 (#1) and 60/40 (#2) mm preserved, leg. Gravier, identified as *Discodoris concinna* by Gravier (MNHN) [these specimens probably are some of the specimens collected by Gravier and that Vayssière (1912) described; the reproductive system was poorly preserved]; **Tanzania**, Dar es Salaam, Harbour entrance, North Reef, 6°48.5′S, 39°18′E, 19 July 1974, four specimens 70/45 (#1), 60/45 (#2), 45/30 (#3) and 42/25 (#4) mm preserved, on sewerage pipe piles, leg. W. B. Rudman, identified as *Discodoris fragilis* by W. B. Rudman (AM C418350); Tanzania, Zanzibar, North end, Ras Nungwi, from lighthouse westward along lagoon formed by barrier reef, 9 November 1994, one specimen 65/50 mm preserved, leg. Don Pisor, unidentified (CASIZ 099383); **Madagascar**, Ile Sainte Marie, reef off Soanambo Hotel, 4 April 1990, three specimens 80/60 (#1), 80/50 (#2) and 50/25 (#3) mm preserved, leg. T. M. Gosliner, identified as *Sebadoris nubilosa* by T. Gosliner (CASIZ 073234) [the two largest specimens were dissected and a piece of notum was cut in specimen #1 prior to the present study]; Madagascar, Mora Mora Village, 5 April 1989, one specimens 40/17 mm preserved [notum missing], leg. T. M. Gosliner, identified as *Sebadoris nubilosa* by T. M. Gosliner (CASIZ 168931) [this specimen, dissected prior to the present study, was formerly part of the lot CASIZ 070352; see *nubilosa*]; **Seychelles**, Mahe Island, 1 km North of Mahe Beach Hotel, 30 April 1984, one specimen 70/55 mm preserved, leg. T. M. Gosliner, identified as *Sebadoris nubilosa* by T. M. Gosliner (CASIZ 074201) [this specimen was dissected prior to the present study; the penis was missing]; Indian Ocean, Seychelles, Aldabra Atoll, Lagoon between Passe Femme and Passe du Bois, 19 March 1986, one specimen 35/25 mm preserved, leg. T. M. Gosliner, identified as *Sebadoris nubilosa* by T. M. Gosliner (CASIZ 074075); Indian Ocean, Seychelles, Mahe Island, 1 km North of Mahe Beach Hotel, 3 May 1984, two specimens 40/30 (#1) and 40/25 (#2) mm preserved, leg. T. M. Gosliner, identified as *Sebadoris nubilosa* by T. M. Gosliner (CASIZ 074248) [both specimens were dissected prior to the present study; the buccal mass and the distal part of the reproductive system were missing in specimen #2]; Indian Ocean, Seychelles, Aldabra Atoll, Lagoon between Passe Femme and Passe du Bois, 19 March 1986, leg. T. M. Gosliner, 5 specimens 50/35 (#1), 50/30 (#2), 50/30 (#3), 50/30 (#4), and 40/25 (#5) mm preserved, identified as *Sebadoris nubilosa* by T. Gosliner, (CASIZ 074193) [the penis of specimen #2 was lost]; **Reunion**, Saint Gilles, 0 to 30 meters depth, [no collecting date], one specimen 43/30 mm preserved, leg. M. Jay (MNHN) [the reproductive system, probably immature, could not be found]; **Australia, Western Australia**, Dampier Arch, 8 meters depth, August 2000, one specimen 55/50 mm preserved, leg. S. Fahey, identified as *Discodoris* by T. M. Gosliner (CASIZ 144022) [this specimen was dissected prior to the present study; the buccal mass was missing and the notum was cut; this lot also contains pieces of notum of two additional specimens]; Australia, Western Australia, Dampier Arch, 16 meters depth, 1 August 2000, one specimen 60/40 mm preserved, identified as *Discodoris fragilis* by S. Fahey (CASIZ 144007) [this specimen was dissected prior to the present study; the reproductive system was missing]; Western Australia, Exmouth Gulf, Learmonth, 22°15′S, 114°05′E, 15 August 1972, two specimens 60/45 and 35/20 mm preserved, leg. N. Coleman, identified as *Discodoris* by W. B. Rudman (AM C418411) [the reproductive system of specimen #2 was present but immature]; **Australia, New South Wales**, Near Coffs Harbour, 30°17.9′S, 153°08.5′E, 1980, one specimen 90/50 mm preserved, leg. R. Simpson, identified as *Discodoris* by W. B. Rudman (AM C126086); Australia, New South Wales, E of Grafton, Minnie Water, 29°46.6′S, 153°18′E, 24 March 1971, one specimen 60/40 mm preserved length, leg. J. Hunter and H. Woodward, identified *Discodoris fragilis* by R. Burn (AM C415874); Australia, New South Wales, Wooli, South East of Grafton, 29°52.1′S, 153°15.9′E, 30 October 1963, two specimens 80/60 (#1) and 50/45 (#2) mm preserved, leg. F. Rost, identified *Discodoris* by W. B. Rudman (AM C418345); Australia, New South Wales, North of Woolgoolga, Arrawarra, 30°03.5′S, 153°12 ′E, 3 December 1990, one specimen 65/40, preserved, leg. Australian Museum party, identified as *Discodoris fragilis* by W. B. Rudman (AM C164559); Australia, New South Wales, East of Grafton, Minnie Water, Middle Reef, 29°46.6′S, 153°18.5′E, 15 February 1965, two specimens 80/55 and 70/35 mm preserved, leg. Australian Museum party, identified as *Discodoris* by W. B. Rudman (AM C416546); Australia, New South Wales, East of Grafton, Minnie Water, 29°46.6′S, 153°18′E, 14 May 1984, one specimen 40/25mm preserved, leg. I. Bennett, identified as *Discodoris* by W. B. Rudman (AM C142252) [the reproductive system was present but immature]; New South Wales, Angourie Pool, 29°29′S, 153°22′E, 11 March 1982, one specimen 60/55 mm preserved, leg. I. Loch, identified as *Discodoris fragilis* by W. B. Rudman (AM C133000); **Australia, Queensland**, Magnetic Island, Cockle Bay, 19°10.6′S, 146°49.4′E, 23 July 1970, one specimen 70/40 mm preserved, leg. I. Loch, identified *Discodoris* by W. B. Rudman (AM C418417); Australia, Queensland, Magnetic Island, Cockle Bay, 19°10.6′S, 146°49.4′E, 6 September 1970, five specimens 80/50 (#1), 70/40 (#2), 65/40 (#3), 65/45 (#4) and 55/37 (#5) mm preserved, leg. I. Loch, identified *Discodoris fragilis* by R. Burn (AM C415872); Australia, Queensland, north side, 8 April 1996, one specimen 45/35 mm preserved, leg. Julie Marshall, identified as *Discodoris concinna* by Robert Burn (NMV F79395); Australia, Queensland, Keepel Bay, Halfway (Middle) Island, 23°12′S, 150°58.2′E, 17 September 1970, two specimens 60/30 (#1) and 45/30 (#2) mm preserved, leg. C. McGonigal, identified *Discodoris* by W. B. Rudman (AM C416544); Australia, Queensland, Great Barrier Reef, Capricorn Group, Heron Island, 23°27′S, 151°55′E, August 1985, one specimen 70/55 mm preserved, leg. G. Avern, identified *Discodoris fragilis* by W. B. Rudman (AM C147842); Australia, Queensland, Magnetic Island, Horseshoe Bay, 19°06.8′S, 146°51.8′E, 22 July 1971, three specimens 70/40 (#1), 50/35 (#2), and 35/20 (#3) mm preserved, leg. I. Loch, identified as *Discodoris* by W. B. Rudman (AM C418416) [no reproductive system was found in specimen #3]; Australia, Queensland, Piccininny Point, 23°13.5′S, 1 50°49′E, 13 September 1970, one specimen 75/45 mm preserved, leg. P. H. Colman, identified as *Discodoris* by W. B. Rudman (AM C418412); Australia, Queensland, Great Barrier Reef, Low Isles, 16°23′S, 145°34′E, October 1928, one specimen 65/40 mm preserved, leg. T. Iredale and G. P. Whitley, identified as *Discodoris* by W. B. Rudman (AM C418348); Australia, Queensland, Townsville, Rowes Bay, 19°14′S, 146°48′E, 21 April 1975, one specimen 55/35 mm preserved, leg. I. Loch, identified as *Discodoris fragilis* by W. B. Rudman (AM C099293); Australia, Queensland, Torres Strait, South side Yam Island, 9°54′S, 142°46′E, 5 July 1976, two specimens 65/35 (#1) and 40/20 (#2) mm preserved, leg. W. F. Ponder, identified as *Discodoris fragilis* by I. Loch (AM C416540); Australia, Queensland, Moreton Bay, Stradbroke Island, 27°30′S, 153°24′E, 14 December 1969, one specimen 35/25 mm preserved, leg. W. F. Ponder, identified as *Discodoris* by W. B. Rudman (AM C416545) [the reproductive system was immature]; Australia, Queensland, Stradbroke Island, off Marine station Dunwich, 17 June 1973, two specimens 90/55 (#1) and 80/60 (#2) mm preserved, leg. B. J. Smith, identified as *Discodoris fragilis* by unknown identifier (NMV F86414); Australia, Queensland, Stradbroke Island, Dunwich Beach, 31 May 1980, one specimen 70/35 mm preserved, leg. B. J. Smith, identified as *Discodoris fragilis* by R. Burn (NMV F86415); Australia, Queensland, Bundaberg, 24°52′S, 152°21′E, May 1901, one specimen 50/40 mm preserved, leg. T. H. May, identified as *Discodoris* by W. B. Rudman (AM C010996) [the notum was cut prior to the present study]; Australia, Queensland, Magnetic Island, Cockle Bay, 19°10.6′S, 146°49.4′E, 22 September 1980, two specimens 70/50 (#1) and 45/35 (#2) mm preserved, leg. I. Loch, identified as *Discodoris fragilis* by I. Loch (AM C418309); Australia, Queensland, Magnetic Island, Picnic Bay, 19°11′S, 145°50.5′E, 1 November 1964, one specimen 45/35 mm preserved, leg. D. F. McMichael and J. C. Yaldwyn, identified as *Discodoris* by W. B. Rudman (AM C418409); Australia, Queensland, Magnetic Island, Horseshoe Bay, 19°06.8′S, 146°51.8′E, 24 September 1980, two specimens 70/45 (#1) and 70/45 (#2) mm preserved, leg. I. Loch and J. Stanisic, identified as *Discodoris* by W. B. Rudman (AM C125915); **Australia, Northern Territory**, Darwin, East Arm, Quarantine Station landing, 12°29′S, 130°54′E, 24 June 1987, one specimen 80/50 mm preserved, leg. W. B. Rudman and party, identified as *Discodoris* by W. B. Rudman (AM C153601); **New Caledonia**, secteur de Touho [Touho and surrounding area], September 1993, one specimen 25/13 mm preserved, leg. Expedition Montrouzier (MNHN, no catalogue number) [the reproductive system was present, but immature]; New Caledonia, secteur de Touho, Baie de Touho et ses environs [Touho and surrounding area], 20°46.5′S, 165°14′E, [station 1252], 1 to 4 meters depth, September 1993, eight specimens 85/60 (#1), 65/40 (#2), 60/40 (#3), 60/40 (#4), 55/35 (#5), 40/30 (#6), 35/17 (#7), 18/14 (#8) mm preserved, leg. Expedition Montrouzier (MNHN, no catalogue number) [the reproductive system of specimens #4 and #7 was present but immature; the reproductive system of specimen #8 was absent]; **Thailand**, Cholburi Province, Bang Saan, 4 August 1958, six specimens 70/50 (#1), 25/16 (#2), 20/15 (#3), 15/10 (#4), 15/10 (#5), and 10/7 (#6) mm preserved, leg. George M. Moore, (USNM 577550) [the reproductive system of specimens #2, #3 and #4 was present but immature; no reproductive system could be found in specimens #5 and #6]; Thailand, Gulf of Thailand, Ko-Sichang, Hin-Tasan, 17 August 1966, two specimens 70/40 (#1) and 55/30 (#2) mm preserved, leg. F. B. Steiner, identified as *Sebadoris nubilosa* by T. M. Gosliner (CASIZ 081897); **Indonesia**, Indo-Malaya, Amboina, [no collecting date], one specimen 45/20 mm preserved, leg. prof. Berghs Efterladenskaber (ZMUC, no catalogue number); **Papua New Guinea**, Port Moresby, Fairfax Harbour, Kanudi, 9°26′S, 147°06′E, 4 September 1967, one specimen 55/35 mm preserved, leg. DAS Fisheries, identified *Discodoris* by W. B. Rudman (AM C418418); **Philippines**, Luzon, Batangas Province, Malajibomanoc Government Lighthouse (Chicken Feather Island), 18 March 1994, one specimen 95/55 mm preserved, leg. M. Miller (CASIZ 096306); **Japan**, Ryukyu Islands, Okinawa, 2.5 km South West of Onna Village, South end of Onna Flats, 26°28.4′N, 127°50.8′E, 1 meter depth, 30 Apr 1987, one specimen 65/45 mm preserved, leg. R.F. Bolland, identified as *Discodoris* by T. Gosliner (CASIZ 070011); **Fiji Islands**, Suva Island, 1918, one specimen 65/50 mm preserved, leg. J. W. Mills, identified as *Discodoris motijerda* [certainly for *D. notiperda*] by unknown identifier (MCZ 048029); **Marshall Islands**, Enewetak Island, lagoon side of island, 3 meters depth, 1 December 1981, one specimen 40/30 mm preserved, leg. Lisa Boucher, identified as *Sebadoris nubilosa* by T. Gosliner (CASIZ 121231) [this specimen had been dissected prior to the present study; the distal part of the reproductive system was missing]; Marshall Islands, Enewetak Island, 4 meters depth, 14 September 1983, three specimen 80/50 (#1), 65/35 (#2), and 35/20 (#3) mm preserved, leg. Scott Johnson, identified as *Sebadoris nubilosa* by T. Gosliner (CASIZ 121232); Pacific Ocean, Marshall Islands, Enewetak Island, lagoon side of island, under dead coral, 3 meters depth, 23 November 1981, one specimen 45/35 mm preserved, leg. Scott Johnson, identified as *Sebadoris nubilosa* by T. M. Gosliner (CASIZ 121234) [this specimen was dissected prior to the present study; the labial cuticle and the distal part of the reproductive system were missing]; **American Samoa**, Tutuila Island, Fagasa Bay, 5 March 1976, one specimen 60/45 mm preserved, leg. Antonio J. Ferreira, identified as *Sebadoris nubilosa* by T. Gosliner (CASIZ 074590).

DISTRIBUTION.— Indo-West Pacific. Red Sea (Ehrenberg 1831, as *granulata*; Gohar and Soliman 1967, as *concinna*; Soliman 1983, as *concinna*; present study; Yonow, 2008), Djibouti, Gulf of Aden (Vayssière 1912 as *concinna*; present study), Tanzania (Edmunds 1971, 1972; present study), Madagascar (present study), Reunion (present study), Mauritius (Quoy and Gaimard 1832, as *sordida*; Abraham 1877, as *sordidata*; Bergh, 1888, as *concinniformis* var.; Pruvot-Fol 1934, as *sordidata*; Yonow and Hayward, 1991), Seychelles (Edmunds 1972; present study), Chagos Archipelago (Eliot 1910a), southeastern India (Rao and Kumary 1974), Sri Lanka (Eliot 1909a, as *frag-*

ilis and *concinna*), eastern India (Alder and Hancock 1864), Thailand (present study), Vietnam (Risbec 1956, as *notiperda* and *noumaea*), South China Sea (Guangyu 1986, as *concinna*), Hong Kong (Orr 1981), Taiwan (Tan et al. 1987), Okinawa, Japan (present study), Philippines (Bergh 1877a, 1884a, as *morphaea*; present study), Indonesia (Bergh 1905, as *rubra* in part), Northern Territory (present study), Papua New Guinea (present study), Vanikoro, Salomon Islands (Pruvot-Fol 1934, as *vanikoro*), Marshall Islands (present study), Samoa Islands (Eliot 1900, present study), Fiji (present study), New Caledonia (present study), Queensland, including the Great Barrier Reef (Willan and Coleman 1984, as *concinna*; Marshall and Willan 1999; Coleman 2001; present study), New South Wales (present study), Abrolhos Islands, Western Australia (O'Donoghue 1924a, as *hedleyi*), Western Australia (Wells and Bryce 1993, as *concinna* and *fragilis*; Coleman 2001, as *Discodoris* sp.; present study). The northernmost localities are in Japan: Okinawa (present study), Japan, and possibly Amakusa (Baba 1933, as *concinna*). The presence of *fragilis* in Sagami Bay (35°N) is problematic (Baba 1949, 1955, as *concinna*). The southernmost locality is 30°17.9′S, 153°08.5′E, New South Wales (AM C126086, present study). The westernmost locality is in the Samoa Islands. Note that *fragilis* is still unknown from Hawaii, French Polynesia, and South Africa. This does not mean that *fragilis* will never be found there, but simply that the current records of *fragilis* from Hawaii, French Polynesia, and South Africa are based on incorrectly identified specimens.

WWW.— The specimens from New Caledonia identified as *Discodoris lilacina* by Bill Rudman (Sea Slug Forum, July 21, 1999, factsheet of *Discodoris lilacina*) are part of *fragilis*. The specimen photographed by Clay Bryce from Dampier Archipelago, Kimberley region, Northwestern Australia, probably is part of *fragilis* (Sea Slug Forum, May 10, 1999, #836). Many other pictures of animals identified as *fragilis* have been posted on different websites, but those doubtful identifications would need to be addressed through dissections.

OCCURRENCE.— The abundance of *fragilis* seems to vary among regions. Based on museum collections, it seems to be more abundant in the Indian Ocean and Queensland than in the rest of the Indo-Pacific, especially in Papua New Guinea, Philippines, or Indonesia. However, two major collecting efforts (CAS and AM collections) certainly introduce an important bias in this preliminary estimation. Therefore, it is difficult to discuss the abundance of *fragilis*. Several authors describe it as a common species (e.g., Rao and Kumary 1974), whereas other authors describe it as being rare in other places (e.g., Marshall and Willan 1999). The fact that the identification of *fragilis* is now much less problematic will certainly ease a survey of its abundance.

HABITAT.— Under rocks in the intertidal zone (Vayssière 1912, as *concinna*), on the sea grass *Cymodocea ciliata* (Rao and Kumary 1974), in rock pools (AM C418345, AM C126086), under coral rubble on muddy fringing reef, intertidal (AM C142252), on boulder in coarse sand and grass patches (AM C418417), reef flat (AM C147842), under rocks (AM C418418, AM C416545, NMV F86414, NMV F86415, NMV F86418), found under stone (USNM 577550), under dead coral (CASIZ 121231, CASIZ 121232), under rock in moat (AM C094252), fringing reef (AM C416540), sand (CASIZ 070011), low tide, rocks, dead coral (CASIZ 081897). Willan and Coleman (1984) consider that *fragilis* is strictly intertidal. This is largely correct, but several specimens were collected below the tidal zone: 0 to 30 meters depth (MNHN Reunion), 1 to 4 meters depth (MNHN, from New Caledonia st. 1252), 3 meters depth (CASIZ 121231, CASIZ 121234), 4 meters depth (CASIZ 121232), from 10 to 20 meters (Vayssière 1912, as *concinna*), 18 meters depth (Bergh 1884, as *morphaea*).

LITERATURE.— Pictures of different color variants have been published under different names: Willand and Coleman (1984, as *concinna*), Guangyu (1986, as *concinna*), Wells and Bryce (1993, as *concinna* and *fragilis*), Marshall and Willan (1999, as *fragilis*), Coleman (2001, as *fragilis* and

"Rosette Discodoris" or *Discodoris* sp.). Rao and Kumary (1974) published an interesting black-and-white picture of the dorsal notum; Gohar and Soliman (1967, as *concinna*) published an accurate drawing of the dorsal color pattern; Tan et al. (1987) also published a color picture of the ventral surface. However, this is the first time that specimens illustrated with color pictures are dissected too. Several radular formulae have been published, but the drawings of lateral teeth are rare and not precise, perhaps except for Edmunds's (1971) illustrations. All anatomical descriptions published are largely incomplete, except for Gohar and Soliman (1967, as *concinna*) and Rao and Kumary (1974). The most important problem with all the descriptions available in the literature is that authors have not paid enough attention to details. In *fragilis* (as in most species), details of the genital anatomy are crucial. The egg ribbons and the development have been studied and illustrated thoroughly by Rao and Kumary (1974) and Gohar and Soliman (1967, as *concinna*). Note that Bergh (1884a), O'Donoghue (1929), Zhongguo (2001) simply mentioned species names (*fragilis* and *stragulata*) in a list of *Discodoris* species without adding new data.

REMARKS ON THE ORIGINAL DESCRIPTION (*granulata*).— The original description is largely incomplete but Ehrenberg described a few features worth mentioning here: dorsal notum dark grey, granulose, with white margins; general shape oblong, rounded; two small oral tentacles digitiform; six bipinnate branchial plumes. The specimen is now homogeneously whitish. It was not dissected. It was opened carefully on the right ventral side, and it clearly has all the diagnostic features of *fragilis* (intestine loop), including its typical reproductive system. Also, its notum is typical of *fragilis* (edges almost ready to fall). Its anterior foot and mouth area (digitiform tentacles) clearly indicate that it is a *Discodorididae*.

REMARKS ON THE ORIGINAL DESCRIPTION (*fragilis*, Figs. 155, 156A-D).— The original description was brief. It is reproduced here in its entirety, with notes added between brackets. "Body broadly oval, depressed, brownish [the dorsal color now is dirty brown, the ventral pigmentation is more distinct]. Cloak ample, firm, covered with minute, somewhat scattered, spiculose, blunt tubercles, of unequal sizes, rather paler than the ground— which is yellowish brown, beautifully marbled with darker brown and white, and covered with minute dark freckles; under surface strongly blotched with reddish brown, the blotches becoming confluent near the foot and fewer towards the margin, which is pale. Dorsal tentacles conical, finely laminated on the upper part [i.e., the rhinophores]; the laminae meeting in front, dark yellowish, much and minutely freckled, especially below; retractile within short sheaths. Oral tentacles linear, pointed [oral tentacles are missing in the types]. Branchial plumes six, large, quadripinnate, minutely speckled with dark brown: the circle open behind: anus large and tubular [six gills are present in one specimen (NEWHM 2002. H2575)]. Foot broad, ovate, reddish brown, with darker blotches, and pale towards the margin: it is deeply grooved in front, but not notched [Eliot (1909a, 1910a) rightly suggested that Alder and Hancock certainly missed the notch of the upper lip of the anterior foot; however, this feature could not be checked because no anterior foot was found in the type material]; the posterior end short and rounded. Length 5 or 6 inches [the only preserved specimen that was not cut in pieces measures 70/45 mm]. Tongue as in *D. tuberculata*, with a prehensile collar. Spicula numerous, small, and rather irregular in form; but usually bent in the centre, with the extremities obtuse, sometimes a little enlarged. Mr Elliot informs us that this species is so brittle that it breaks to pieces even when alive [*fragilis* is indeed well known for breaking pieces of its notum]. The two specimens preserved are much mutilated. It is uncommon, and bears some resemblance to the *D. bellicosa* of Kelaart, from which it differs in size and colour, as well as in the obtuse form of the tubercles. The spawn is white, and in the form of a single irregular coil, with the free margin much contorted [the spawn is not present in the type material]." The labial cuticle is armed with two sickle-shaped jaws. Rodlet tips are irregularly rounded or pointed. The radular formulae are: 29 × (55/65-0-55/65) on the slide 3/23/04, and 37 × (75/85-0-75/85) on the slide 3/23/32. For the same slides, Eliot (1906b) observed a radula of 30 × (55-0-55) and a radula with 40 rows (without number of teeth per half row). The rachidian teeth are absent and the rachidian space is narrow. The size of the teeth is constant, although it tends to increase gradually towards the edges; the size of the five or six outermost teeth decreases gradually. All teeth are hamate; the outermost tooth may be vestigial.

Remarks on the original description (*stragulata*, Figs. 154A-B).— The type currently is colorless: the dorsal notum is dirty grey, with fuzzy darker areas (dark spots cannot be distinguished); the ventral surface also is dirty grayish. Several features mentioned by Abraham could be verified, such as the presence of rounded tubercles on the entire surface of the dorsal notum, six branchial plumes, a bilabiate anterior foot with a notched upper lip, etc. The tubercles are hard, not soft as in *Sebadoris nubilosa*. Two external features must be commented on: the "6-lobed margin" of the branchial sheath is not comparable to a six-lobed branchial sheath of *Platydoris* or *Asteronotus* species; the margin of the gill sheath is not smooth, but it surely is not deeply lobed. Also, the "flat, linear, pointed" oral tentacles actually are flattened, but surely not ear-shaped as in *Asteronotus raripilosa*. The number of rhinophoral lamellae could not be determined. The anatomy of the reproductive system could not be determined because of the poor preservation. However, the bursa copulatrix is much larger than the receptaculum seminis. Two important internal characters were observed: the secondary, thick, muscular layer of the dorsal mantle, and the intestine with a ventral loop. The radula was not mounted for SEM because the type locality is unknown anyway.

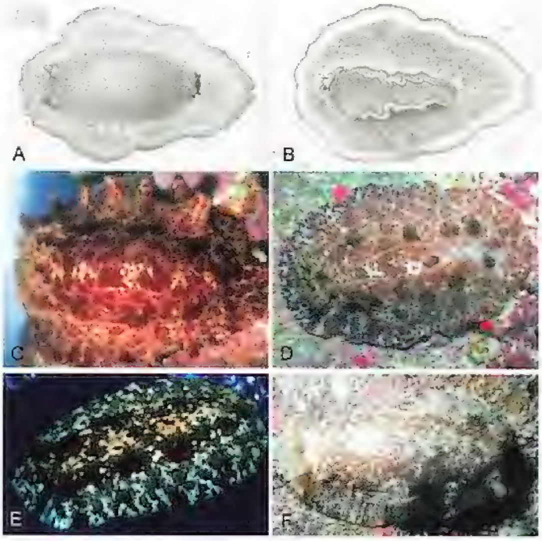

Figure 154. *Sebadoris fragilis*. A. Dorsal view, original illustration of *Doris stragulata*, after Abraham (1877: plate XXVIII, fig. 7), total length = 70 mm.— B. Ventral view, original illustration of *Doris stragulata*, after Abraham (1877: plate XXVIII, fig. 8), total length = 70 mm.— C. Dorsal view, CASIZ 099383, Tanzania, total length (preserved) = 65 mm.— D. Dorsal view, CASIZ 074201, Seychelles, total length (preserved) = 70 mm.— E. Dorsal view, CASIZ 070011, Japan, total length (preserved) = 65 mm.— F. Dorsal view, CASIZ 073234, Madagascar, total length (preserved) = 80 or 50 mm (three specimens in lot).

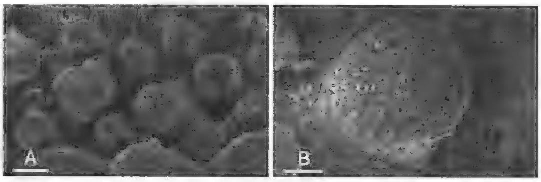

Figure 155. *Sebadoris fragilis*, dorsal notum, syntypes. A. Tubercles, scale = 200 µm.— B. Tubercle, scale = 100 µm.

Remarks on the original description (*morphaea*).— The type currently is homogeneously whitish-yellowish. The dorsal notum is covered with tubercles that are rounded or conical. The anterior foot is bilabiate, the upper lip is notched, and the oral tentacles are digitiform. The branchial sheath is well marked, but not lobed. Bergh mentioned several features that could not be verified here because the organs are missing, such as 40/50 rhinophoral lamellae, two jaw plates, and a radular formula of 39 × (75-0-75). The number of lamellae is significantly higher than usual (thirty lamellae). Lamellae, however, sometimes are difficult to count; also, Bergh sometimes counted more lamellae than there probably were (e.g., *Discodorididae coerulescens*). The general organization of the reproductive system drawn by Bergh is similar to the reproductive system found in other specimens of *fragilis*: Bergh mentioned a 2 mm long penis, but it seems that this length also included the complete penial complex, with the penial sheath. The intestine, although it was separated from the digestive gland presents a distinct loop that, given its length, certainly was in a ventral position. Also, traces of the position of the intestine can still be observed upon the digestive gland, and there clearly is a mark of ventral loop.

Remarks on the origincal description (*sordidata*, Figs. 158A-B).— The holotype, briefly described by Quoy and Gaimard, was re-examined and redescribed by Pruvot-Fol (1934), who thought that it probably was part of *fragilis*. Quoy and Gaimard's brief description is given here in its entirety (my translation): "The shape and the color of this species is a little bit similar to a Onchidie. It is slightly coriaceous and has a rounded back. The mantle is much larger than the foot; both of them are oval. The mouth is prominent; its appendages are small. The entire surface of the body is verrucose, covered with grayish and whitish, with two or three brown spots on the edges of the mantle. The hyponotum adjacent to the foot is dark gray. The foot is yellow, dotted with light brown. This mollusk lives in the Ile-de-France [Reunion Isl.]. One can find it on the îlots aux Cerfs. Its length is two and a half inches. It is one those [mollusks] that have the capacity to autotomize part of its mantle." The holotype currently is colorless: homogeneously light grayish, dirty cream. It already was colorless when Pruvot-Fol re-examined it. As pointed out by Pruvot-Fol, the mantle of the holotype is complete, although Quoy and Gaimard wrote that this species had the capacity to autotomize its mantle (suggesting that they probably saw several specimens). The dorsal tubercles, in poor condition, have various shapes and sizes. The oral tentacles are digitiform. The anterior foot is bilabiate and the upper lip is notched. Pruvot-Fol dissected and illustrated some radular teeth, similar to the teeth observed here in *fragilis*. Unfortunately, she did not indicate the radular formula. Several internal features were examined. The intestine is long, coiled ventrally. The reproductive system is exactly the same as the reproductive system found in all specimens of *fragilis*. In particular, the fertilization duct presents the diagnostic loop upon the bursa copulatrix. The penis (which may not be complete) measures less than 1 mm in length, and is unarmed.

Remarks on the original description (*rubra*).— These remarks are based only on the paralectotype, not the lectotype. Bergh provided a brief description of the external morphology of this specimen. The dorsal notum and the ventral surface both present the commonest color pattern of *fragilis*. The dorsal tubercles are not soft, *nubilosa*-like papillae. The intestine presents a long ventral loop. The caecum of the stomach is large. Bergh did not indicate the radular formula.

Remarks on the original description (*hedleyi*, Figs. 156E-F).— The dorsal notum presents the commonest pattern in *fragilis*, though faded due to preservation: overall dark appearance, and a mottling of dark blotches of various sizes and shapes. The hyponotum bears large, dark blotches; the foot is intensely pigmented too. The tubercles, of various sizes and shapes, are not caryophyllidia. The foot is bilabiate and the upper lip is notched. There are about twenty-five rhinophoral lamellae in the large specimen (rhinophores are missing in the specimen that was cut in pieces). O'Donoghue described six branchial plumes. O'Donoghue did not notice any jaw plates. He probably overlooked them. The illustration of the radular teeth by O'Donoghue is accurate, and the radular formula he provides is correct: 30 × (55/60-0-55/60) was found here and he proposed 33/35 × (57-0-57). O'Donoghue described a hermaphroditic gland independent from the digestive gland, as in *Alloiodoris marmorata*, the type species of the genus where he allocated *hedleyi*. However, the hermaphroditic gland clearly covers the digestive gland, as in the vast majority of discodorid species. It is *not* a discrete, independent organ, as in *Alloiodoris marmorata* or *Discodorididae coerulescens*. The reproductive system of *hedleyi* has the diagnostic feature of *fragilis*, the loop of the fertilization duct, and has the same general organization (elongated, bent receptaculum seminis, bursa copulatrix much larger than the receptaculum seminis, etc.). O'Donoghue

(1924a:548) described a penis "armed with a series of rows of hooks." Unfortunately, the shape of the penis could not be checked because the distal part of the reproductive system is missing. I do not take O'Donoghue's observation should probably not be taken for granted for a couple of reasons: 1) it could not be verified; 2) he did not draw this penis; 3) he made a mistake that is difficult to explain with the hermaphroditic gland.

Remarks on the original description (*vanikoro*, Figs. 158C-D).— The original description of *vanikoro* is based on a specimen misidentified by Quoy and Gaimard (1832) as *Doris maculosa* Cuvier, 1804. Quoy and Gaimard briefly described the color (my translation): "on each side of the [back of the] body [i.e., each side of the median line], two rows of irregular black patches, on a grey-greenish spooted ground color. The undersurface of the mantle also is spotted with brown patches and dots (...) The foot is red-brown with brown dots." They also mentioned a few external features, such as the presence of small oral tentacles with a yellow tip, and six branchial plumes. The specimen currently is homogeneously cream-yellowish. As Pruvot-Fol pointed out, the dorsal tubercles are of various shapes and sizes. The anterior foot is bilabiate and the upper lip is notched. The shape of the radular teeth could not be addressed because the radula is missing. Pruvot-Fol found a formula of 39 × (79-0-79). It is unclear whether or not the intestine has a ventral loop because the intestine was cut by Pruvot-Fol. The reproductive system presents the two diagnostic features of *fragilis*, i.e., the loop of the fertilization duct, and the conical penis. Its general organization is the same as the organization found in *fragilis*: an elongated, bent receptaculum seminis, an ampulla convoluted with many tight loops, etc.

Remarks on the original description (*notiperda*, Figs. 157, 159).— The eight specimens currently are homogeneously yellowish-cream. Risbec rightly mentioned a character observed so far only in *fragilis*: the mantle is composed of two layers, a thin external layer, and a thick muscular layer around the body cavity. Risbec proposed that the autotomization of the mantle was particularly easy in *notiperda* because only the thin layer is broken. This proposition could make sense. Risbec mentioned several other characters, such as six branchial plumes, about thirty rhinophoral lamellae, bilabiate anterior foot with the upper lip notched, oral tentacles elongated and flattened, an armed labial cuticle, intestine with a long, ventral loop, radular rows with a total of 150 teeth, i.e., 75 teeth per half row. In the lectotype, dissected here, the radular formula is 26 × (67-0-67). The general organization of the reproductive system of *notiperda* is the same as in *fragilis*. In particular, the penis is small (0.6 mm long in the lectotype) and conical, and the fertilization duct presents the diagnostic loop upon the bursa copulatrix. Risbec drew the loop of the fertilization duct, but did not recognize its taxonomic importance.

Remarks on the original description (*concinniformis* var.).— The original description of the variety of *concinniformis* is similar to the description of *concinniformis* (see that species). According to Bergh, the specimen measured 65/45 mm, which is correct; there are 60 to 70 rhinophoral lamellae; the radular formula is 40 × (75-0-75); the receptaculum seminis measures 10/0.8 mm, and the bursa copulatrix 7.5/2.5 mm. Bergh regarded this specimen as a variety of *concinniformis* because of the color, especially the color of the ventral surface: the margin of the hyponotum is dark blue; the foot sole is blue-grey. Now, the specimen is homogeneously white. Its notum is typical of *fragilis* (very fragile edges that are ready to break).

Description of new specimens (Figs. 160-188).— *Color*. Only four pictures of live animals were available for the present study. The overall appearance of the dorsal notum of live animals is dark brown (from dark reddish to black), but the dorsal notum actually is mottled with dark spots of various shapes and sizes on a cream ground color. Sometimes, but not always, pairs of dark spots are present on both sides of the median line. The gills are light brown, cream, with a lighter margin. Rhinophores are light or dark brown, possibly with a cream apical knob. There was no picture

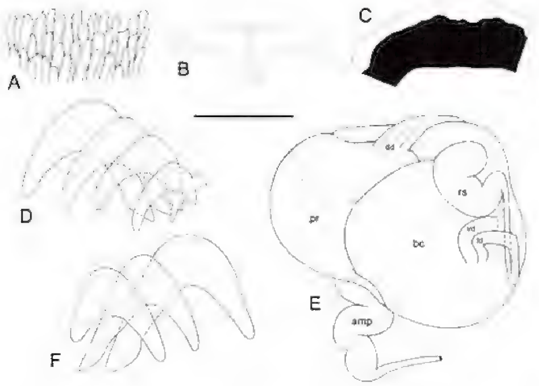

FIGURE 156. *Sebadoris fragilis*, types. A. Jaw rodlets, syntype of *Doris fragilis* (labeled *Doris bellicosa*), slide NEWHM 3/23/07, scale = 50 µm.— B. Jaws, syntype of *Doris fragilis* (labeled *Doris bellicosa*), slide NEWHM 3/23/07, scale = 370 µm.— C. Segment of hyponotum, syntype of *Doris fragilis*, NEWHM 2002.H2575, scale = 20 mm.— D. Outermost teeth, syntype of *Doris fragilis* (labeled *Doris bellicosa*), slide NEWHM 3/23/04, scale = 120 µm.— E. Reproductive system, syntype of *Alloiodoris hedleyi*, NHM 1922.925.18-19, scale = 2.2 mm.— F. Outermost teeth, syntype of *Alloiodoris hedleyi*, slide NHM 1923.3.27.9, scale = 75 µm.

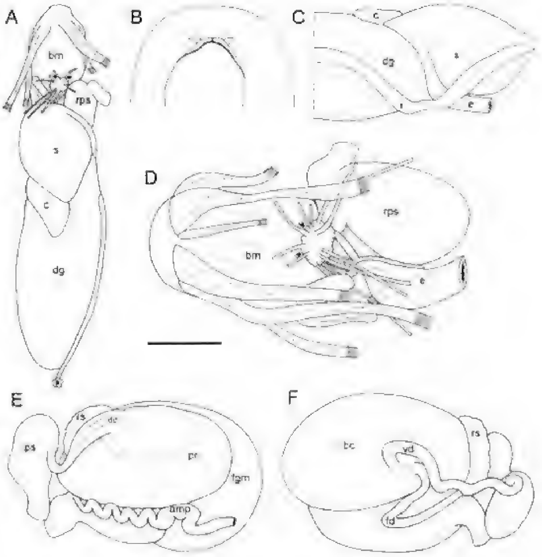

FIGURE 157. *Sebadoris fragilis*, lectotype of *Discodoris notiperda*. A. General anatomy, scale = 6.5 mm.— B. Anterior, ventral surface, scale = 13 mm.— C. Esophagus, stomach, and intestine, lateral view, scale = 4.3 mm.— D. Anterior, general anatomy, scale = 6.5 mm.— E. Reproductive system, scale = 2 mm.— F. Reproductive system, scale = 2 mm.

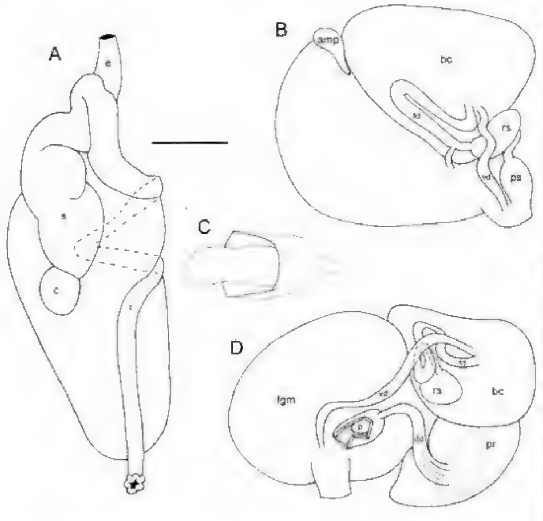

FIGURE 158. *Sebadoris fragilis*, types. A. Digestive system (except buccal mass), holotype of *Doris sordidata*, scale = 3.3 mm.— B. Reproductive system, holotype of *Doris sordidata*, scale = 5.5 mm.— C. Penis, holotype of *Discodoris vanikoro*, scale = 1 mm.— D. Reproductive system, holotype of *Discodoris vanikoro*, scale = 3.7 mm.

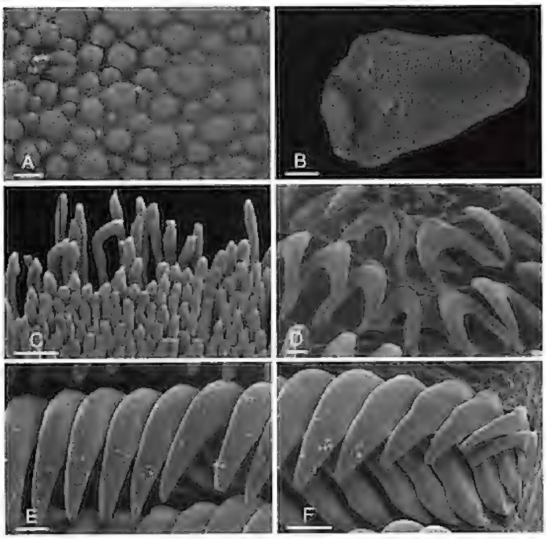

FIGURE 159. *Sebadoris fragilis*, lectotype of notiperda, MNHN. A. Tubercles, scale = 200 µm.— B. Penis, scale = 100 µm.— C. Jaw rodlets, scale = 20µm.— D. Innermost teeth, scale = 20 µm.— E. Median teeth, scale = 40 µm.— F. Outermost teeth, scale = 40 µm.

available for the ventral surface of live animals. The color of preserved specimens is informative. Many specimens have a dorsal color pattern similar to live animals (mottling of dark and cream spots, with an overall dark appearance); this color pattern still is distinct, even when the dark spots are faded due to preservation. Specimens from only three localities have two distinct, darker rows of spots between the rhinophores and the gills, in addition to the general mottling. Specimens from only two localities are homogeneously cream, with no traces of dark spots. Note that several old types also are homogeneously cream, which suggests that specimens tend to loose their color gradually. The color of the ventral surface of preserved specimens also is informative. Most specimens have an overall dark appearance on both the hyponotum (due to a mottling of large spots of various shapes and sizes) and the foot (due to numerous dark dots); many specimens also have a more or less regular continuous dark band on the hyponotum, usually adjacent to the lateral sides of the foot.

External morphology. The body is oval. The length equals less than twice the width. The length of the preserved specimens dissected ranges from 10 mm (USNM 577550 #6) to 90 mm (NMV F86414 #1, AM C126086) and 95 mm (CASIZ 096306). However, only fourteen specimens measured less than 40 mm long. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform and not grooved. In many specimens, the mid-dorsal notum is composed of two layers that can separate easily: an internal, thick muscular layer, and the external, thin layer of mantle. Regardless of the presence of two distinct layers, the notum often is much thicker than usual (Table 2). The dorsal notum bears tubercles that are not caryophyllidia. Those tubercles have an irregular shape, conical or hemispherical. Their size varies within a single notum too. The number of spicules protruding from the surface of the tubercles varies among individuals, and even within a single notum (it also varies because of the variation): some tubercles are almost smooth, and some are covered with spicules. Many small holes (diameter <10 µm) and many tufts of cilia are present on the dorsal surface, including the rhinophores and the gills. When the notum is well preserved, tubercles have a heavily ciliated apex. In preserved specimens, the margins of the rhinophoral and branchial sheaths are smooth or lightly crenulate. There are six tri- or quadripinnate branchial plumes. In large specimens, the gill sheath may be slightly lobed, but it never is deeply lobed and star-shaped (as in *Platydoris* species). The rhinophores have from ten to thirty lamellae, depending on the size of the animal, but usually from twenty to twenty-five lamellae.

Digestive system. The stomach is free, large, on top of the left, anterior side of the digestive gland. The caecum, always present except for one specimen (AM C133000), is much larger in all other discodorid species considered in the present study. In a few cases, however, the caecum is small, as in other species (CASIZ 099383, AM C126086, AM C416545, USNM 577550 #4 and #5, CASIZ 121231); note that several of these specimens were immature, which suggests that the normal, adult caecum of *fragilis* is large. In the vast majority of the specimens, the intestine is not straight and dorsal: it is convoluted with at least one long, tight loop, and often several additional smaller loops (e.g., AM C418309, CASIZ 096306). The long loop normally folds under the ventral surface of the digestive gland. However, in a few specimens, the intestinal loop is located on the right lateral side of the digestive gland (CASIZ 074193 #1, #2, and #3, CASIZ 170083, CASIZ 074248, AM C133000, AM C099293, AM C010996), USNM 577550 #2 and #3), not under its ventral surface. In a few specimens, the intestinal loop is loose, instead of tight, and dorsal, instead of lateral (CASIZ 074075, CASIZ 074193 #4 and #5, AM C415412, NMV F86415, USNM 577550 #4 and #5). Interestingly, the specimens (except for AM C415412 and NMV F86415) whose intestinal loop is loose and dorsal are small, which suggests that a normal, adult intestinal loop is tight and dorsal or lateral. Note that the two specimens AM C415412 and NMV F86415 have a typical

TABLE 2. Individual variation of morphological features (see Text) in *Sebadoris fragilis*: the median dorsal notum (DN) is normal (n), thick (t) or with a double layer (d); the caecum (Cae) is small (s), significantly large (l), in between (m), or absent (a) although the specimen was not dissected prior to the present study; the reproductive system (RS) is mature (m), poorly preserved (pp), present but immature (i), absent (a) although the specimen was not dissected prior to the present study (i.e., completely immature), or missing (mi) because the specimen was dissected prior to the present study; the intestinal loops (IL) are located on the right, ventral side of the digestive gland (v), on the right, lateral side of the digestive gland (l), or on the dorsal side of the digestive gland (d); the prostate (Pr) is divided in two (2) or three (3) parts; the penis is conical (c), elongated (e), coiled (co), absent (a) although the specimen was not dissected prior to the present study, or missing (mi) because the specimen was dissected prior to the present study; the deferent duct (DD) is coiled (c) or straight (s); for all features, a dash indicates that data could not be obtained (because the organs were missing).

Cat. #	**Locality**	**Spm #**	**Size**	**DN**	**Cae**	**RS**	**IL**	**Pr**	**Penis**	**DD**
			(mm)							
fragilis	East. India	Synt.	-	t	-	mi	-	-	-	-
stragulata	Unknown	Holot.	70/40	d	l	pp	v	-	-	-
vanikoro	Vanikoro	Holot.	75/55	n	-	m	v	-	c	c
notiperda	Vietnam	Lect	55/30	d	l	m	v	3	c	s
sordidata	Mauritius	Holot.	60/35	t	l	m	v	3	c	c
rubra	Indonesia	Paral.	75/35	-	l	mi	l	-	-	-
hedleyi	Abrolhos Is.	Synt.	-	n	l	m	-	2	mi	s
CASIZ 170083	Red Sea		35/20	n	-	m	l	2/3	e	s
MNHN	Djibouti	1	80/50	d	l	m	v	2.3	c	s
		2	60/40	d	l	m	v	2/3	c	s
CASIZ 099383	Tanzania		65/50	n	s	m	v	3	c	s
AM C418350	Tanzania	1	70/45	d	-	m	v	3	c	c
		2	60/45	d	-	m	v	-	c	c
		3	45/30	d	-	m	v	3	c	c
		4	42/25	d	-	i	v	-	a	c
CASIZ 073234	Madagascar	1	80/60	t	s	m	v	3	c	s
		2	80/50	t	l	m	v	3	c	s
		3	50/25	t	l	m	v	3	c	s
CASIZ 168931	Madagascar		40/17	d	l	m	v	2/3	c	s
CASIZ 074201	Seychelles		70/55	t	l	m	v	3	mi	s
CASIZ 074075	Seychelles		35/25	n	l	m	d	3	e	s
CASIZ 074248	Seychelles	1	40/30	n	l	m	l	2/3	e	c
		2	40/25	n	l	m	l	2/3	mi	c
CASIZ 074193	Seychelles	1	50/35	n	l	m	l	-	c	c
		2	50/30	n	l	m	l	3	e	s
		3	50/30	n	l	m	l	3	c	c
		4	50/30	n	l	m	d	2/3	co	c
		5	40/25	n	l	m	d	3	e	s
MNHN	Reunion		43/30	d	l	a	v	-	-	-
CASIZ 144022	WA		55/50	t	l	m	v	3	c	s

TABLE 2 (continued). For explanation, see table header, p. 153.

Cat. #	Locality	Spm #	Size (mm)	DN	Cac	RS	IL	Pr	Penis	DD
CASIZ 144007	WA		60/40	t	l	mi	v	-	-	-
AM C418411	WA	1	60/45	t	-	m	v	3	c	c
		2	35/20	t	l	i	v	-	a	s
AM C126086	NSW		90/50	t	s	pp	v	3	-	-
AM C142252	NSW		40/25	n	l	i	v	-	a	c
AM C416546	NSW		80/55	d	l	m	v	-	c	c
			70/35	d	l	m	v	3	c	c
AM C133000	NSW		60/55	d	a	m	l	3	c	c
AM C153601	North. Terr.		80/50	t	m	m	v	3	c	c
AM C418417	Queensland		70/40	t	m	m	v	3	c	c
NMV F79395	Q.		45/35	t	m	m	v	3	c	s
AM C415872	Q.		80/50	d	l	m	v	3	c	s
			70/40	d	l	m	v	3	c	s
			65/40	d	l	m	v	3	c	s
			65/45	d	l	m	v	3	c	s
			55/37	d	l	i	v	-	a	s
AM C416544	Q		60/20	t	l	m	v	3	c	c
			45/30	t	l	m	v	3	c	s/c
AM C147842	Q		70/55	t	l	m	v	3	c	s/c
AM C418416	Q	1	70/40	n	l	m	v	3	c	s
		2	50/35	t	l	m	v	3	c	s
		3	35/20	t	l	i	v	-	a	-
AM C418412	Q.		75/45	d	l	m	d	3	c	s
AM C418348	Q.		65/40	d	l	m	v	3	e	s
AM C099293	Q		55/35	t	l	m	l	3	e	s
AM C418309	Q.	1	65/35	n	l	m	v	3	c	s
		2	45/35	t	l	m	v	3	c	s
AM C418409	Q.		45/35	t	a	pp	v	3	c	-
AM C125915	Q.	1	70/45	t	l	m	v	3	c	s
		2	70/45	t	l	m	v	3	c	s
AM C416540	Q.	1	65/35	t	l	m	v	3	c	s/c
		2	40/20	t	l	m	v	3	c	c
AM C416545	Q		35/25	n	s	i	v	-	a	-
NMV F86414	Q.	1	90/55	d	l	m	v	3	c	c
		2	80/60	d	l	m	v	3	c	c
NMV F86415	Q.		70/35	d	m	m	d	3	c	s

TABLE 2 (continued). For explanation, see table header, p. 153.

Cat. #	Locality	Spm #	Size (mm)	DN	Cae	RS	IL	Pr	Penis	DD
AM C010996	Q.		50/40	t	l	m	l	3	c	s
AM C418418	PNG		55/35	d	l	m	v	3	c	c
MCZ 048029	Fiji		65/50	t	l	pp	-	-	c	c
MNHN	NC-1252	1	85/60	d	m	m	v	3	c	s
		2	65/40	n	l	m	v	3	c	s
		3	60/40	n	l	m	v	3	e	s
		4	60/40	d	l	m	v	2/3	c	s
		5	55/35	n	s	m	v	3	c	s
		6	40/30	d	m	m	v	3	c	s
		7	35/17	d	m	i	v	-	a	-
		8	18/14	d	l	a	v	-	-	-
USNM 577550	Thailand	1	70/50	t	l	m	v	3	c	s
		2	25/16	n	l	i	l	-	c	c
		3	20/15	n	l	i	l	-	c	c
		4	15/10	n	s	i	d	-	a	c
		5	15/10	n	s	a	d	-	-	-
		6	10/7	n	s	a	d	-	-	-
CASIZ 081897	Thailand	1	70/40	t	l	m	v	3	c	c
		2	55/30	t	l	m	v	3	c	c
ZMUC	Indonesia		45/20	n	l	m	v	3	c	c
CASIZ 096306	Philippines		95/55	n	m	m	v	3	a	c
CASIZ 070011	Japan		65/45	n	l	m	v	3	c	c
CASIZ 074590	Samoa		55/45	n	l	m	v	3	c	c
CASIZ 121231	Marshall		40/30	n	s	m	v	3	mi	c
CASIZ 121232	Marshall	1	80/50	d	l	m	v	2/3	c	c
		2	65/35	t	l	m	v	-	c	c
		3	35/20	n	-	m	v	3	c	c
CASIZ 121234	Marshall		45/30	n	-	m	-	-	mi	c

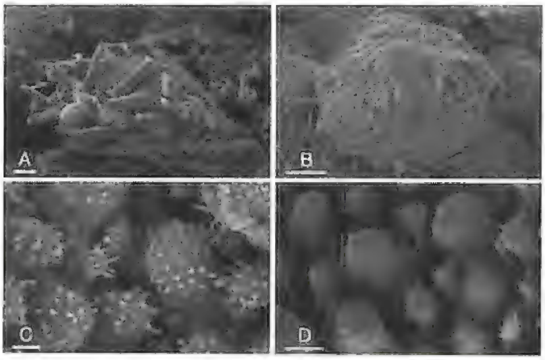

FIGURE 160. *Sebadoris fragilis*, dorsal notum. A. CASIZ 070011, scale = 30 μm.— B. CASIZ 070011, scale = 100 μm.— C. AM C415872 (#3), scale = 60 μm.— D. AM C415874, scale = 100 μm.

penis of *fragilis*. Finally, note that the intestinal loop is always present. The labial cuticle is armed with a pair of lateral jaw plates. Rodlet tips are irregular. A labial cuticle that seemed to be smooth under the dissecting microscope also was smooth with the SEM, suggesting that jaw plates can exceptionally be absent (CASIZ 099383). The structure (armed *vs* smooth) of another labial cuticle (CASIZ 121232 #2) is unclear, although it seems unarmed. A total of 38 radulae have been prepared for SEM. The length of the radula equals or is slightly higher than its width. The radular sac cannot be seen by dorsal dissection. The variation of the radular formulae is presented in Table 3. The number of rows and the number of teeth per half row clearly increases with the size of the animals. The three smallest radulae are found in the smallest specimens: 14 × (27-0-27) in a 10 mm long specimen, 18 × (38-0-38) in a 15 mm long specimen, and 21 × (34-0-34) in a 18 mm long specimen. The largest radulae are found in the largest specimens: 35 × (75-0-75) in a 90 mm long specimen (NMV F86414), and 39 × (85-0-85) in a 95 mm long specimen (CASIZ 096306). Only two radulae have less than 20 rows and only six radulae have less than 40 teeth per half row. The rachidian teeth are absent and the rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the teeth gradually increases towards edges, and gradually

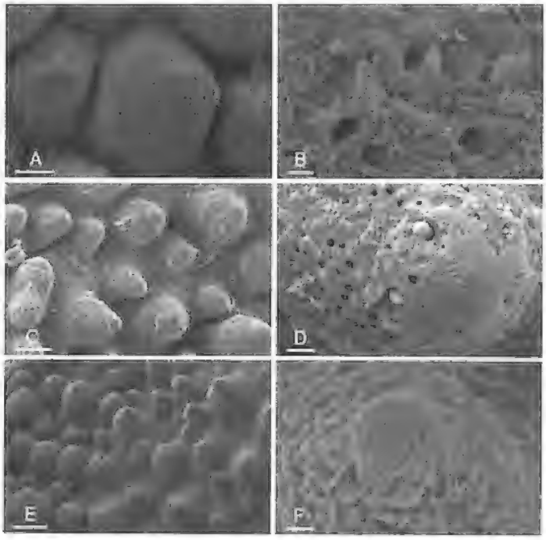

FIGURE 161. *Sebadoris fragilis*, dorsal notum. A. CASIZ 074248 (#1), scale = 100 μm.— B. CASIZ 074248 (#1), scale = 10 μm.— C. CASIZ 074193 (#2), scale = 200 μm.— D. CASIZ 074193 (#2), scale = 20 μm.— E. CASIZ 074193 (#3), scale = 200 μm.— F. CASIZ 074193 (#3), scale = 20 μm.

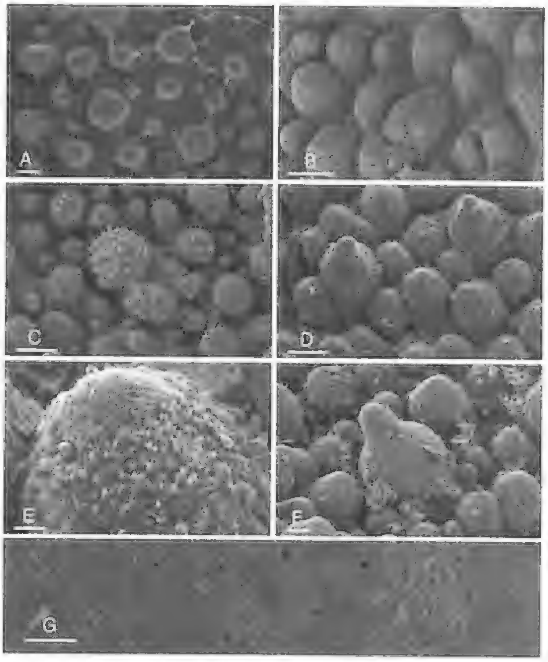

FIGURE 162. *Sebadoris fragilis*, dorsal notum. A. CASIZ 073234 (#1), scale = 200 μm.— B. MNHN (#2), st. 1252, scale = 200 μm.— C. AM C418417, scale = 200 μm.— D. CASIZ 074201, scale = 200 μm.— E. CASIZ 074201, scale = 50 μm.— F. CASIZ 099383, scale = 100 μm.— G. CASIZ 099383, scale = 10 μm.

decreases after three fourth of the length. The three or five outermost teeth are smaller than the rest of the lateral teeth. The last outermost tooth often is reduced and not hamate. The lateral teeth bear no denticles.

Nervous system. The circum-esophageal nerve ring is short. Its length equals up to two times the dorsal width of the ganglia. The fusion of the cerebral, pleural, and pedal ganglia varies: ganglia are separated or more or less fused. The surface of the ganglia is smooth, although some spherical masses are sometimes distinguishable through the thin, transparent tissue covering the ganglia. Those ganglionic masses are not external.

Reproductive system. A reproductive system was found in almost all specimens. However, out of 14 specimens measuring less than 40 mm in length, three have no reproductive system, eight have an immature (i.e., small, with organs poorly or partly developed) reproductive system, and three have a globally mature reproductive system. Note that no reproductive system system was found in a 43 mm long specimen (MNHN Reunion), and that an immature reproductive system was found in a 55 mm long specimen (AM C415872 #5), a 42 mm long specimen (AM C418350 #4), and a 40 mm long specimen (AM C142252). The ampulla is tightly convoluted (from five to twelve loops), even in young specimens with an immature reproductive system. It enters immediately into

TABLE 3. Radular formulae of specimens of *Sebadoris fragilis* (Alder and Hancock, 1864) dissected for the present study.

Cat. #	Locality	Spm #	Size (mm)	Radular formula
CASIZ 170083	Red Sea		35/20	20 ´ (40-0-40)
MNHN	Djibouti	1	80/50	29 ´ (67-0-67)
CASIZ 099383	Tanzania		65/50	28 ´ (48-0-48)
CASIZ 073234	Madagascar	1	80/60	28 ´ (65-0-65)
		2	80/50	30 ´ (70/75-0-70/75)
		3	50/25	29 ´ (65/70-0-65/70)
CASIZ 168931			40/17	30 ´ (58-0-58)
CASIZ 074201	Seychelles		70/55	36 ´ (50-0-50)
CASIZ 074075			35/25	20 ´ (45-0-45)
CASIZ 074248		1	40/30	33 ´ (55-0-55)
CASIZ 074193		1	50/35	38 ´ (65-0-65)
		2	50/30	21 ´ (42-0-42)
		3	50/30	37 ´ (55-0-55)
		4	50/30	26 ´ (54-0-54)
		5	40/25	20 ´ (46-0-46)
AM C418411	Western Australia	1	60/45	36 ´ (66-0-66)
		2	35/20	26 ´ (55-0-55)
AM C415874	New South Wales		60/40	33 ´ (61-0-61)
AM C418345		1	80/60	27 ´ (62-0-62)
AM C153601	Northern Territory		80/50	26 ´ (52-0-52)
AM C418417	Queensland		70/40	35 ´ (70/75-0-70/75)
AM C415872		3	65/40	33 ´ (70-0-70)
AM C418416		3	35/20	29 ´ (57-0-57)
AM C125915		1	70/45	33 ´ (72-0-72)
AM C416545			35/25	25 ´ (48-0-48)
NMV F86414		1	90/55	35 ´ (75-0-75)
MNHN (1252)	New Caledonia	2	65/40	26 ´ (65/70-0-65/70)
		8	18/14	18 ´ (38-0-38)
notiperda	Vietnam	Lect	55/30	28 ´ (65-0-65)
USNM 577550	Thailand	1	70/50	32 ´ (75-0-75)
		4	15/10	21 ´ (34-0-34)
		6	7-Oct	14 ´ (27-0-27)
CASIZ 096306	Philippines		95/55	39 ´ (85-0-85)
CASIZ 070011	Japan		65/45	29 ´ (60-0-60)
CASIZ 074590	Samoa		55/45	29 ´ (49-0-49)
CASIZ 121231	Marshall Isl.		40/30	30 ´ (44-0-44)
CASIZ 121232		2	65/35	34 ´ (56-0-56)

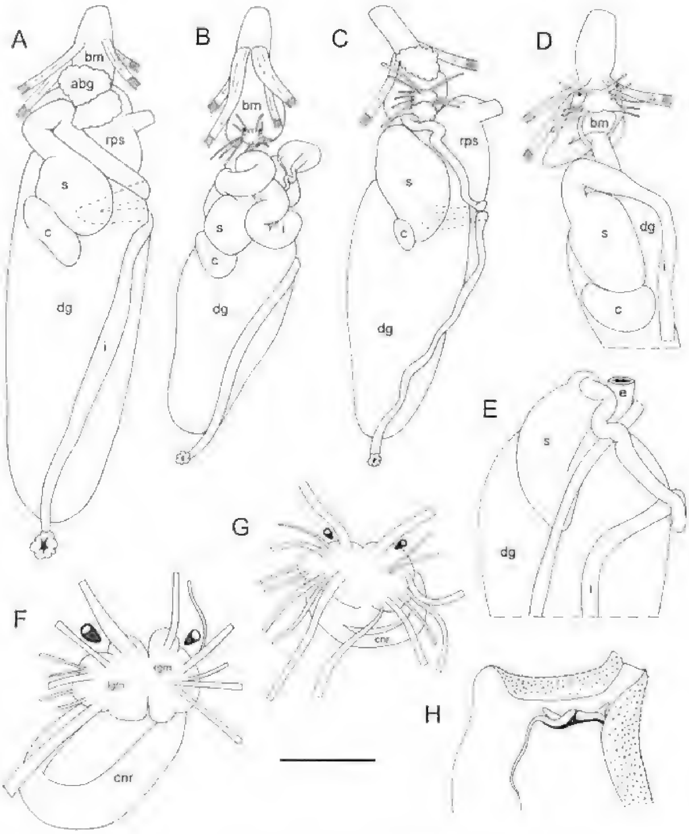

FIGURE 163. *Sebadoris fragilis*. A. General anatomy, CASIZ 074193 (#2), scale = 6 mm.— B. General anatomy, MNHN (st. 1252, #2), scale = 10 mm.— C. General anatomy, AM C415874, scale = 10 mm.— D. General anatomy (posterior part not represented), CASIZ 074248 (#1), scale = 5 mm.— E. Lateral view of the intestine, CASIZ 070011, scale = 7.5 mm.— F. Nervous system, MNHN (st. 1252, #2), scale = 2 mm.— G. Nervous system, AM C415874 (#3), scale = 2 mm.— H. Anterior, ventral view, CASIZ 070011, scale = 12 mm.

the female gland mass. The division between male and female ducts cannot be seen by dissection. In most specimens (Table 2), the prostate is divided in three parts of different (and variable) color: the proximal part is whitish, the median part is whitish-yellowish, and the distal part is yellowish-orange. However, for various reasons (e.g., maybe preservation), these parts are sometimes not distinguishable. The deferent duct is straight or loosely convoluted (Table 2). The deferent duct ends by a distinct, unarmed penis, protected within a penial sheath that occasionally is much larger that the penis itself (e.g., AM C415874, MNHN st.1252 #2, AM C153601). In the vast majority of the specimens, the penis has a conical shape, with an apical hole. The penis sizes ranges from 0.1 mm long (USNM 577550 #2) up to 1 mm (e.g., AM C418412, CASIZ 073234 #2). Most penises measure around 0.5 mm, but their size always is less than 1 mm. Only one elongated penis measures 1.3 mm exactly. The conical shape varies among specimens: penises are wider than long or longer than wide, with a rounded apex, with a pointed apex, etc. There are a few elongated, cylindrical penises (e.g., MNHN st.1252 #3, CASIZ 074193 #5), but these forms are easy to derive from a basic, conical shape. In one locality from the Seychelles (CASIZ 074193 #1 to #5), penises were more variable, and probably less typical than average: two basic conical penises, a coiled penis (the only one found in *fragilis* so far), and two elongated penises, especially one with a heavily ciliated apex. However, the great variation found among the penises of these five specimens from the same locality shows that these shapes, though unusual, are just individual variants of the basic, common, conical shape. No distal accessory gland was found. The vaginal duct is straight or loosely convoluted. The fertilization duct is convoluted. However, the position of its loops is peculiar and diagnostic of the reproductive system of *fragilis*. All the specimens referred to as *fragilis* here share this peculiar position of the fertilization duct. Although this position is difficult to represent in words, it can be described as follows: the fertilization duct has a distinct, U-shaped loop upon the surface of the bursa copulatrix, before it disappears into the female gland mass. The disappearance of the fertilization duct into the female gland mass is marked by a distinct duct. The length of the duct of the receptaculum

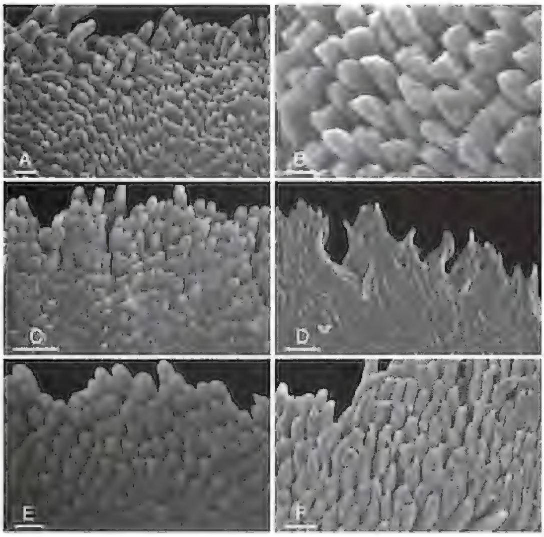

FIGURE 164. *Sebadoris fragilis*, jaws. A. CASIZ 070011, scale = 10 µm.— B. CASIZ 074590, scale = 5 µm.— C. CASIZ 074201, scale = 20 µm.— D. MNHN (#1), Djibouti, scale = 20 µm.— E. MNHN (#8), st. 1252, scale = 10 µm.— F. MNHN (#2), st. 1252, scale = 10 µm.

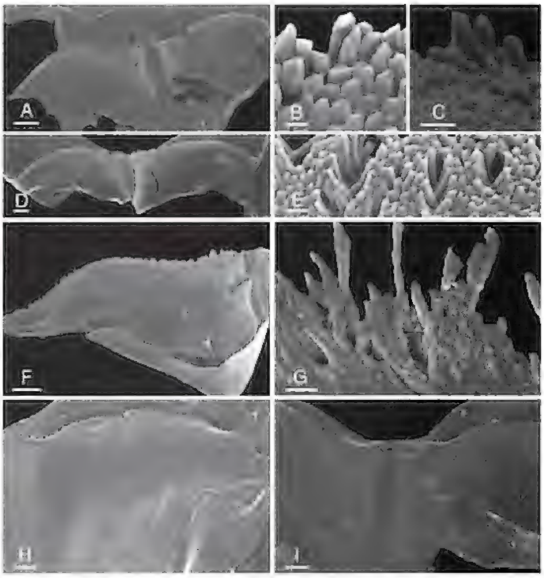

FIGURE 165. *Sebadoris fragilis*, jaws. A. Two jaw plates, CASIZ 074248 (#1), scale = 200 µm.— B. CASIZ 074248 (#1), scale = 5 µm.— C. CASIZ 074193 (#3), scale = 10 µm.— D. AM C416545, scale = 100 µm.— E. AM C415872 (#3), scale = 10 µm.— F. Left, lateral jaw plate, AM C415872 (#3), scale = 200 µm.— G. AM C418417, scale = 10 µm.— H. Right, possibly smooth, labial cuticle, CASIZ 121232 (#2), scale = 200 µm.— I. Smooth labial cuticle, CASIZ 099383, scale = 200 µm.

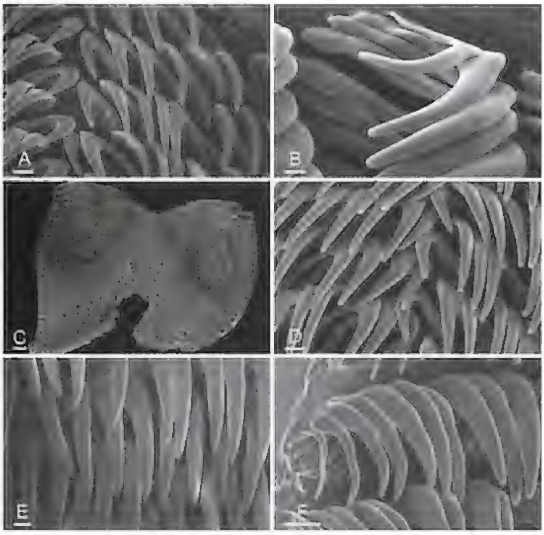

FIGURE 166. *Sebadoris fragilis*, radula. A. Innermost teeth, CASIZ 074201, scale = 20 µm.— B. Outermost teeth, CASIZ 168931, scale = 10 µm.— C. CASIZ 073234 (#2), scale = 200 µm.— D. Innermost teeth, CASIZ 073234 (#2), scale = 20 µm.— E. Median teeth, CASIZ 073234 (#3), scale = 20 µm.— F. Outermost teeth, CASIZ 073234 (#3), scale = 30 µm.

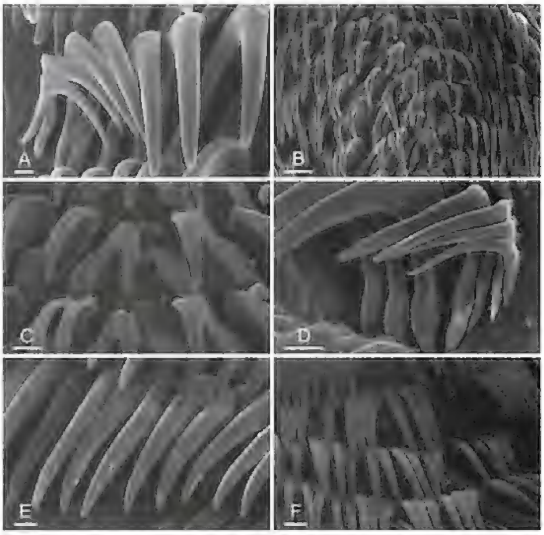

FIGURE 167. *Sebadoris fragilis*, radula. A. Outermost teeth, CASIZ 074075, scale = 10 µm.— B. Innermost teeth, CASIZ 074075, scale = 40 µm.— C. Innermost teeth, CASIZ 074193 (#2), scale = 20 µm.— D. Outermost teeth, CASIZ 074193 (#2), scale = 20 µm.— E. Median teeth, CASIZ 074193 (#2), scale = 20 µm.— F. Median teeth, CASIZ 074193 (#3), scale = 30 µm.

seminis varies a great deal among specimens. In all (but three) specimens, the bursa copulatrix is at least ten times as large as the receptaculum seminis: the bursa copulatrix is slightly larger than the receptaculum in two specimens (MCZ 048029, USNM 577550 #5); it is twice as large as the receptaculum in one specimen (CASIZ 121232 #1). The bursa copulatrix is spherical-ovate in all specimens. The receptaculum seminis is elongated in all specimens, except for two specimens from New South Wales (AM C418345) where the receptaculum is spherical. In many specimens, the receptaculum is slightly bent. The two spermatic pouches are tightly close to one another.

DIAGNOSTIC FEATURES.— The best diagnostic features of *fragilis* are found in the genital anatomy: the small, conical penis (< 1 mm in length) and the general organization of the reproductive system (especially the loop of the fertilization duct) are distinguishable. The digestive system is informative. The intestine has a long, ventral loop only in *Sebadoris nubilosa* and *fragilis*, although a loop on the lateral side of the digestive gland is found occasionally in other species (e.g., *Discodorididae branneri*). Note, however, that a ventral loop is not found in all specimens (Table 2) and thus is not strictly diagnostic. Also, the notum of the animal must be checked carefully in order to avoid a misidentification with *nubilosa*. The color should be used cautiously (i.e., in combination with other, exclusive features) because it varies among specimens and can be confused with several other species. The dark forms of *fragilis* may be confused with *Asteronotus raripilosa* (e.g., Thompson 1975), but *raripilosa* has branched dorsal papillae and a six-lobed branchial sheath that are absent in *fragilis*; they also can be confused with *nubilosa*, but *nubilosa* has distinguishable, soft, dorsal papillae. The dark forms of *fragilis* cannot be confused with *Tayuva lilacina*, but the light forms may be confused with it. However, the dark spots on the dorsal notum of *lilacina* are well delineated, and not connected with multiple smaller, darker dots (see *Tayuva lilacina*), whereas the dorsal notum of the light forms of *fragilis* always have a dark, overall appearance with a mottlings of numerous dots and spots of various sizes and shapes. Generally speaking, *Tayuva lilacina* is the species with which *fragilis* has often been confused.

Here, a series of differences is discussed, which should help avoid confusion in the future. Penial morphology and genital anatomy allow clear-cut identifications. However, a few features that can be observed more easily are discussed. The length is helpful: only eight specimens (out of 92) of *Sebadoris fragilis* measured less than 40 mm, whereas only six specimens (out of 63) of *Tayuva lilacina* measured more than 40 mm; in average (at least in the Indo-West Pacific), *fragilis* specimens are much longer than *lilacina* specimens; if preserved specimens measure more than 60 mm, they have little chance to be part of *lilacina* (note that *lilacina* tends to be larger in Hawaii than in the rest of the Indo-West Pacific). Combining sexual maturity and animal size might be helpful: out of fourteen *fragilis* specimens measuring less than 40 mm in length, only three had a fully mature reproductive system, and none of the specimens measuring less than 35 mm had a fully mature reproductive system; in *lilacina*, only specimens measuring less than 8 mm may occasionally have an immature reproductive system (see *Tayuva lilacina*). The radula also is informative. The number of teeth per half row probably is the most useful character: *lilacina* never has more than 40 teeth per half row (at least in the Indo-West Pacific) whereas only three radulae were found with less than 40 teeth per half row in *fragilis*. The number of teeth per half row should not be used to make clear-cut decision but it should be of great help in rejecting some identifications: in other words, the fact that a radula has more than 50 teeth per half row implies that the specimen has little chance to be part of *lilacina*, but does not imply that the specimen is part of *fragilis*. Finally, one cannot discuss *fragilis* without mentioning its capacity to autotomize its lateral, dorsal notum, which, by the way, explains its species name (note that Risbec created the name *notiperda*, synonym of *fragilis*, for the same reason). Autotomization is not found exclusively in *fragilis*. Many other species have the capacity to autotomize part of their dorsal mantle, such as *Peltodoris*

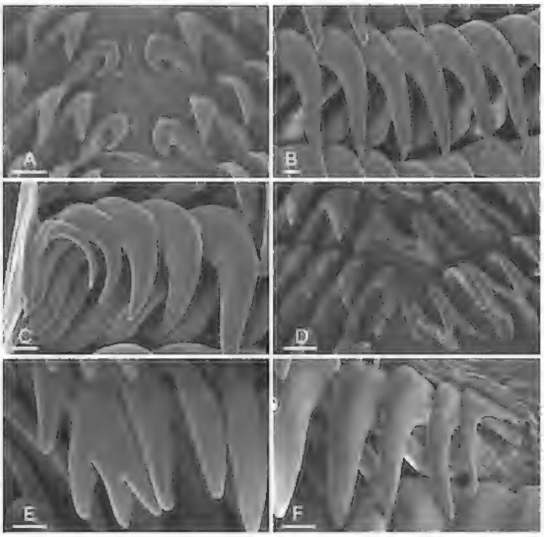

FIGURE 168. *Sebadoris fragilis*, radula. A. Innermost teeth, CASIZ 121232 (#2), scale = 40 μm.— B. Median teeth, CASIZ 121232 (#2), scale = 20 μm.— C. Outermost teeth, CASIZ 121232 (#2), scale = 20 μm.— D. Innermost teeth, CASIZ 121231, scale = 40 μm.— E. Median teeth, CASIZ 121231, scale = 20 μm.— F. Outermost teeth, CASIZ 121231, scale = 20 μm.

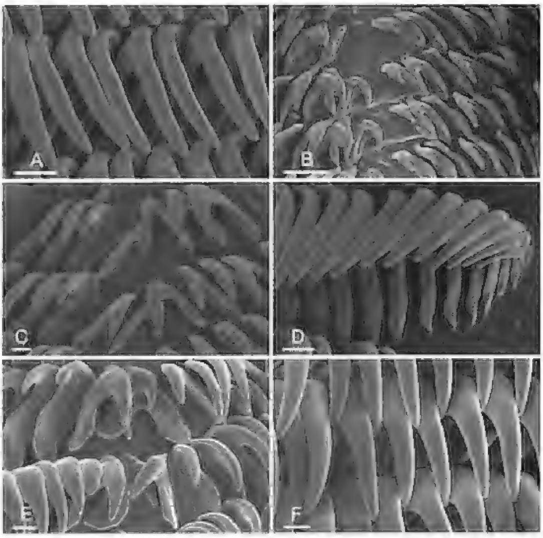

FIGURE 169. *Sebadoris fragilis*, radula. A. Median teeth, CASIZ 096306, scale = 100 μm.— B. Innermost teeth, CASIZ 096306, scale = 100 μm.— C. Innermost teeth, CASIZ 121234, scale = 20 μm.— D. Outermost teeth, CASIZ 121234, scale = 30 μm.— E. Innermost teeth, CASIZ 074590, scale = 20 μm.— F. Median teeth, CASIZ 074590, scale = 20 μm.

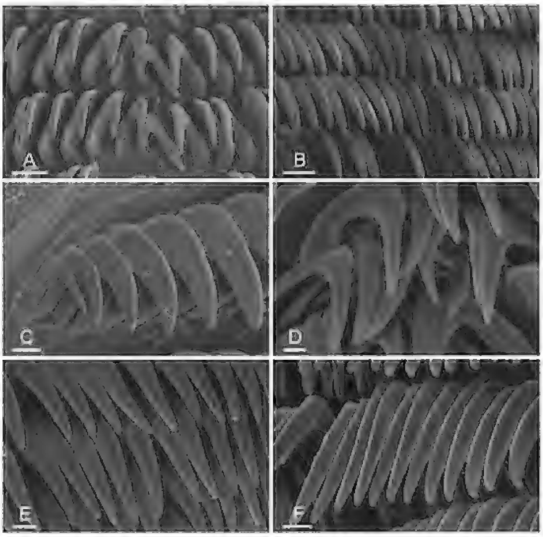

FIGURE 170. *Sebadoris fragilis*, radula. A. Innermost teeth, MNHN, Touho st. 1252 (#2), scale = 60μm.— B. Median teeth, MNHN, Touho st. 1252 (#2), scale = 100μm.— C. Outermost teeth, MNHN, Touho st. 1252 (#2), scale = 30 μm.— D. Innermost teeth, MNHN, Touho st. 1252 (#8), scale = 10 μm.— E. Median teeth, MNHN, Touho st. 1252 (#8), scale = 20 μm.— F. Median teeth, CASIZ 070011, scale = 40 μm.

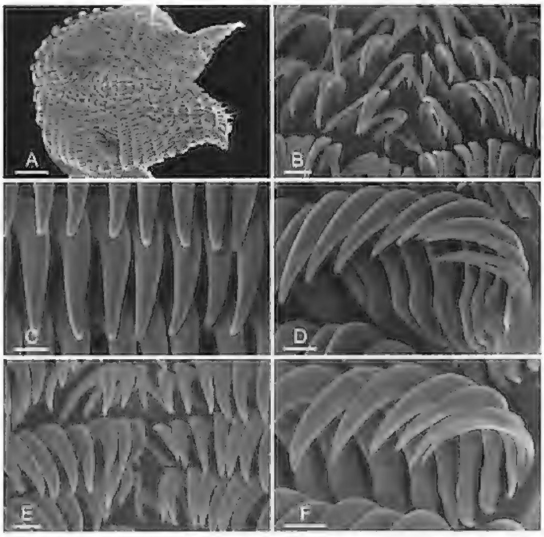

FIGURE 171. *Sebadoris fragilis*, radula. A. NMNH 577570 (#4), scale = 200 μm.— B. Innermost teeth, NMNH 577570 (#4), scale = 20 μm.— C. Median teeth, NMNH 577570 (#4), scale = 20 μm.— D. Outermost teeth, NMNH 577570 (#4), scale = 20 μm.— E. Innermost teeth, NMNH 577570 (#6), scale = 20 μm.— F. Outermost teeth, NMNH 577570 (#6), scale = 20 μm.

atromaculata and *Discodoris boholiensis*. However, only *fragilis* seems to be able to loose its entire ring of lateral notum. Risbec (1956, as *notiperda*) rightly pointed out that this capacity might be related to a peculiar structure of the mantle: indeed, the body cavity of *fragilis* is embedded within a thick mucular layer, on top of which is the thin, external notum; as a result, the median part of the dorsal notum is much thicker than the lateral ring, which can easily break.

INFRA-SPECIFIC CHARACTER VARIATION.— Here the individual variation that is known in *fragilis* is presented, based on new observations (see above) and the existing literature (only specimens regarded as *fragilis* are considered, see discussion).

The smallest specimens known are described in the present study: seven specimens shorter than 25 mm long. Eliot (1909a, as *concinna*) and Edmunds (1971) also mentioned 26 mm long specimens. Fourteen specimens measure from 80 to 95 mm long, i.e., probably from 100 to 120 mm long, alive. Gohar and Soliman (1967, as *concinna*) found live animals measuring from 90 to 150 mm long; Edmunds (1971) found live animals measuring from 26 to 105 mm long; Eliot (1910a) found a preserved specimen measuring 90 mm long. In summary, specimens measuring more than 100 mm in length are common.

The dorsal mottling of brown areas upon a yellowish background varies among individuals. The overall appearance of the dorsal notum is dark, but the intensity of this darkness varies. Several authors (e.g., Eliot 1909a, as *concinna*; Gohar and Soliman 1967, as *concinna*; Edmunds 1971; Rao and Kumary 1974) noticed that the median part of the dorsal notum was often darker than the lateral ring and that longitudinal rows of dark patches could be present on either side of the median line. These two features, however, vary among individuals. On the hyponotum, all authors have mentioned the presence of large brown blotches often united into a ring adjacent to the foot. The foot is dark. Most authors have observed that the tip of the brownish rhinophores was whitish. The range of variation for the number of rhinophoral lamellae observed here (from 10 to 30) is broader than what is found in the literature —from 17 to 30 (e.g., Gohar and Soliman 1967, as *concinna*; Edmunds 1971; Rao and Kumary 1974). The 45 rhinophoral lamellae described by Bergh (1877a) in the original description of *morphaea* could be a mistake. Several authors have noticed that the margin of the gill sheath could be lobed. However, the lobes are never as deep as in *Platydoris* or *Asteronotus* species: Rao and Kumary (1974:691) described "six angular facets;" Eliot (1910a:422) described a gill sheath "obscurely six-lobed;" and Gohar and Soliman (1967:202) described "six shallow grooves." Most authors have noticed an intense capacity to autotomize the mantle. Eliot (1900) mentioned specimens that would loose their complete lateral, mantle ring.

A total of 56 radular formulae are known for *fragilis* (including 38 radulae from the present study). Three radular formulae are available from the original descriptions of *morphaea*, *hedleyi*, and *vanikoro* (incomplete radular formula described by Risbec for *notiperda* not considered). Three additional radular formulae are described here for types of *fragilis* (though Eliot published some data on the radulae of the types of *fragilis*) and *notiperda*. Finally, eleven radular formulae are available in the literature (original descriptions not included). The smallest radulae were observed in the present study, certainly because no small specimen was dissected previously: 14 × (27-0-27) in a 10 mm long specimen, 18 × (38-0-38) in a 15 mm long specimen, and 21 × (34-0-34) in a 18 mm long specimen (Table 3). The maximum number of rows observed was 39 (in a 95 mm long specimen). However, radulae with more than 40 rows are not rare: 56 × (90/100-0-90/100) in a 90 mm long specimen, preserved, from the Chagos Archipelago (Eliot 1910a); 48 × (88-0-88) in a maximum 150 mm long specimen, alive, from the Red Sea (Gohar and Soliman 1967, as *concinna*); 45 × (75-0-75) in a 75 mm long specimen, preserved, from Sri Lanka (Eliot 1909a); from 30 to 45 rows and from 69 to 80 teeth per half row in maximum 110 mm long specimens, alive, from southeastern India (Rao and Kumary 1974). The maximum numbers of teeth per half row are:

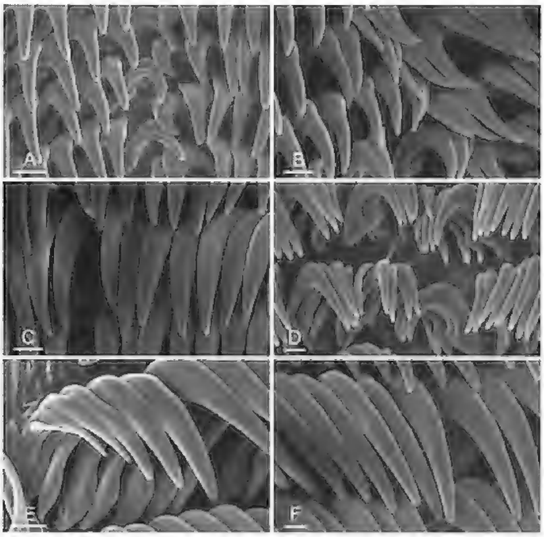

FIGURE 172. *Sebadoris fragilis*, radula. A. Innermost teeth, AM C418411 (#1), scale = 40 µm.— B. Innermost teeth, AM C418411 (#2), scale = 20 µm.— C. Median teeth, AM C418416 (#2), scale = 30 µm.— D. Innermost teeth, AM C418411 (#3), scale = 20 µm.— E. Outermost teeth, AM C418416 (#3), scale = 20 µm.— F. Median teeth, AM C418416 (#3), scale = 20 µm.

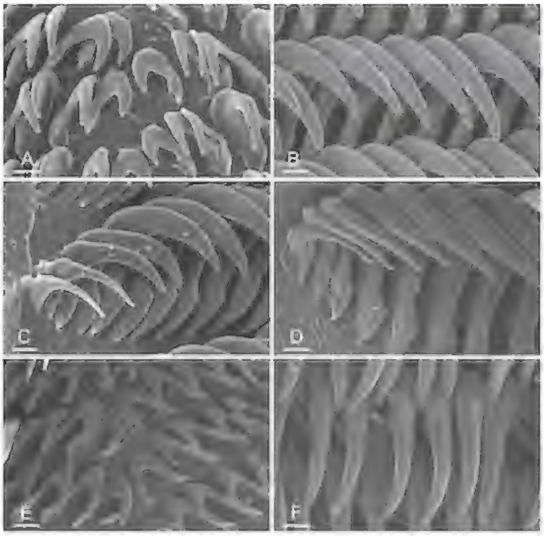

FIGURE 173. *Sebadoris fragilis*, radula. A. Innermost teeth, CASIZ 074248 (#1), scale = 20 µm.— B. Median teeth, CASIZ 074248 (#1), scale = 20 µm.— C. Outermost teeth, CASIZ 074248 (#1), scale = 20 µm.— D. Outermost teeth, CASIZ 099383, scale = 30 µm.— E. Innermost teeth, CASIZ 099383, scale = 40 µm.— F. Median teeth, CASIZ 099383, scale = 40 µm.

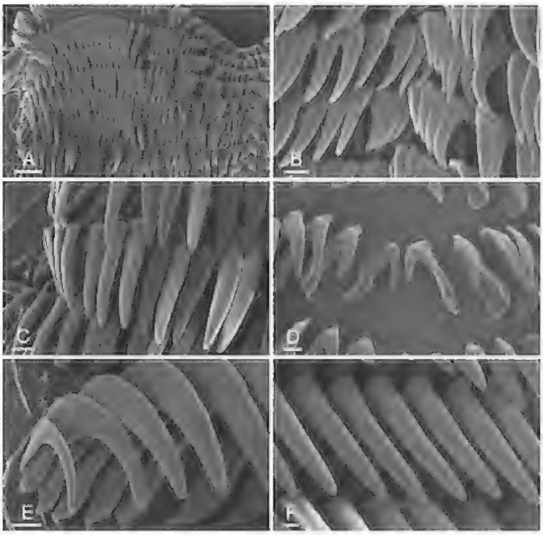

FIGURE 174. *Sebadoris fragilis*, radula. A. Left rows, CASIZ 170083, scale = 100 µm.— B. Innermost teeth, CASIZ 170083, scale = 20 µm.— C. Outermost teeth, CASIZ 170083, scale = 20 µm.— D. Innermost teeth, MNHN Djiboutti (#1), scale = 20 µm.— E. Outermost teeth, MNHN Djiboutti (#1), scale = 20 µm.— F. Median teeth, MNHN Djiboutti (#1), scale = 20 µm.

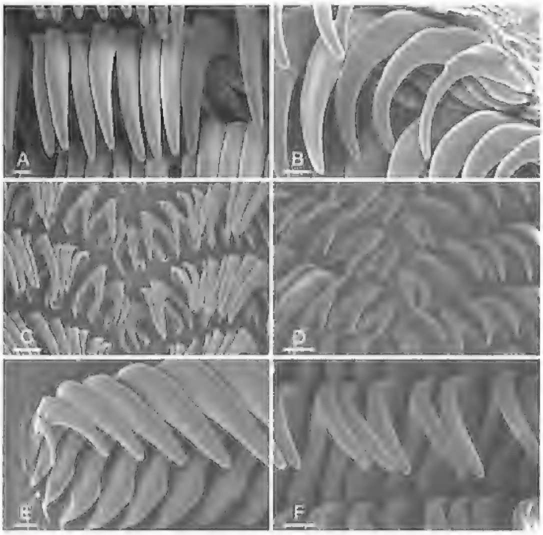

FIGURE 175. *Sebadoris fragilis*, radula. A. Median teeth, AM C415874, scale = 20 µm.— B. Outermost teeth, AM C415874, scale = 20 µm.— C. Innermost teeth, AM C415874, scale = 40 µm.— D. Innermost teeth, AM C415872 (#3), scale = 40 µm.— E. Outermost teeth, AM C415872 (#3), scale = 20 µm.— F. Median teeth, AM C415872 (#3), scale = 40 µm.

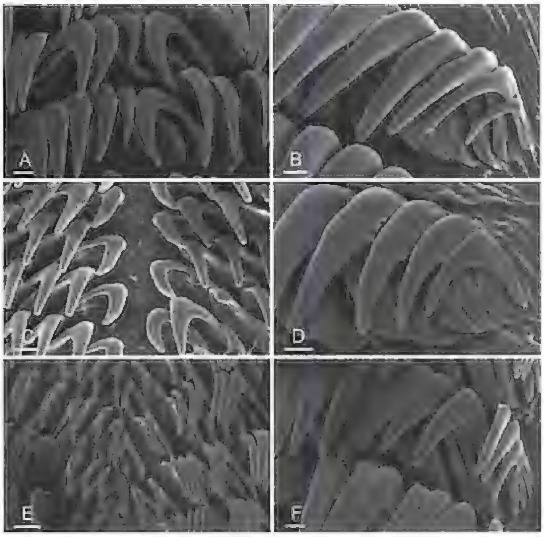

FIGURE 176. *Sebadoris fragilis*, radula. A. Innermost teeth, AM C418345 (#1), scale = 20 µm.— B. Outermost teeth, AM C125915 (#1), scale = 20 µm.— C. Innermost teeth, AM C153601, scale = 40 µm.— D. Outermost teeth, AM C418417, scale = 20 µm.— E. Innermost teeth, AM C416545, scale = 40 µm.— F. Outermost teeth, AM C416545, scale = 20 µm.

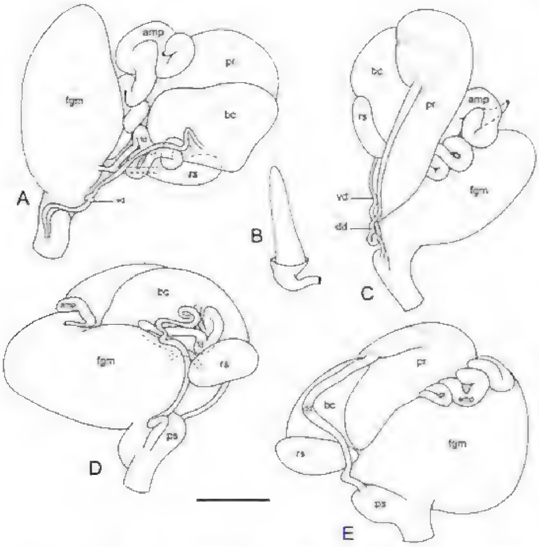

FIGURE 178. *Sebadoris fragilis*, reproductive system. A. CASIZ 074193 (#3), scale = 3.4 mm.— B. Penis, CASIZ 074193 (#3), scale = 0.9 mm.— C. CASIZ 074193 (#3), scale = 3.4 mm.— D. CASIZ 074193 (#2), scale = 5 mm.— E. CASIZ 074193 (#2), scale = 5 mm.

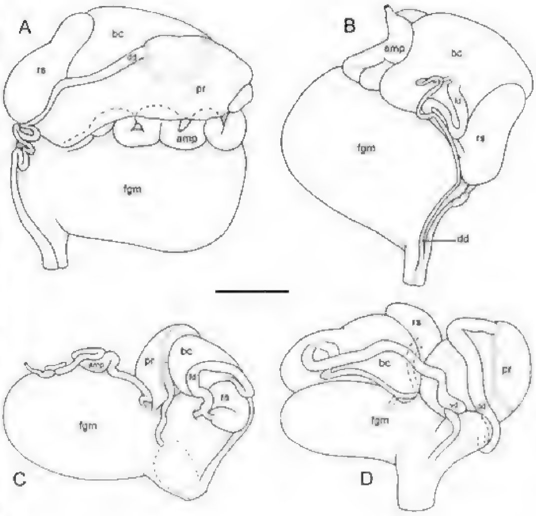

FIGURE 177. *Sebadoris fragilis*, reproductive system. A. CASIZ 074248 (#1), scale = 2.6 mm.— B. CASIZ 074248 (#1), scale = 2.6 mm.— C. CASIZ 074201, scale = 5 mm.— D. CASIZ 099383, scale = 3 mm.

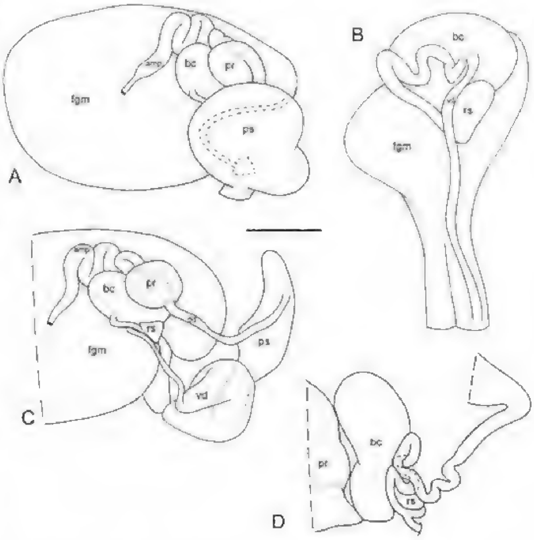

FIGURE 179. *Sebadoris fragilis*, reproductive system. A. AM C153601, scale = 5 mm.— B. AM C418411 (immature individual), scale = 1.5 mm.— C. AM C153601 (organs were moved), scale = 6 mm.— D. Spermatic pouches, AM C153601, scale = 3 mm.

90/100 (Eliot 1910a), 88 (Gohar and Soliman 1967, as *concinna*; present study), 75/85 (type material of *fragilis* described here), and 80 (Rao and Kumary 1974). Finally, only a few authors (Bergh 1884a, as *morphaea*; Eliot 1910a; Rao and Kumary 1974) described the ventral loop of the intestine, simply because most authors did not describe the intestine.

The available data on genital anatomy in the existing literature are rare. The illustrations of the reproductive system by Bergh (1884a, as *morphaea*), Rao and Kumary (1974), Gohar and Soliman (1967, as *concinna*) show a bursa copulatrix that is much larger than the receptaculum. The drawing by Edmunds (1971) illustrates a bursa that is only two or three times larger than the receptaculum, but his drawing is schematic. All penises observed here measured less than 1 mm in length, except for one 1.2 mm long penis. Rao and Kumary (1974) and Gohar and Soliman (1967, as *concinna*) illustrated a small, conical penis. The 3 mm long praeputium mentioned by Bergh (1884a, as *morphaea*) and the "large" penis mentioned by Gohar and Soliman (1967) likely designate the complete penial sheath. Finally, note that Eliot (1909a, as *concinna*) described a 26 mm long specimen that was immature, which is compatible with the present observations.

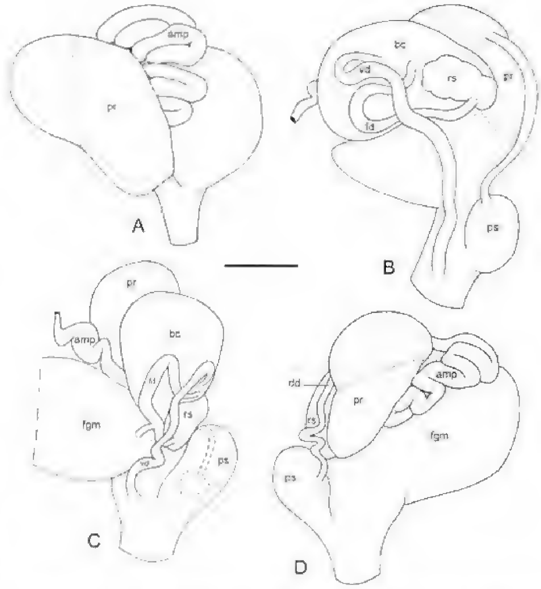

FIGURE 180. *Sebadoris fragilis*, reproductive system. A. CASIZ 070011, scale = 3.7 mm.— B. AM C415872 (#3), scale = 0.6 mm.— C. AM C415874, scale = 3.7 mm.— D. AM C415874, scale = 3 mm.

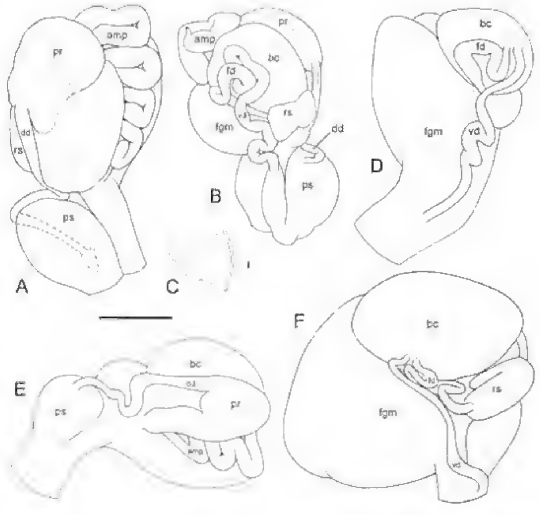

FIGURE 181. *Sebadoris fragilis*, reproductive system. A. MNHN (st. 1252, #2), scale = 2.7 mm.— B. MNHN (st. 1252, #2), scale = 3 mm.— C. Penis, MNHN (st. 1252, #2), scale = 1.5 mm.— D. NMNH 577550 (#2), scale = 0.4 mm.— E. NMNH 577550 (#2), scale = 0.5 mm.— F. CASIZ 121232 (#2), scale = 3.7 mm.

DISCUSSION.— So far, the taxonomy of *Sebadoris fragilis* has been extremely complicated, to say the least. In both literature and collections, the name *fragilis* was given to specimens that were not part of *fragilis*, and specimens that were not part of *fragilis* were identified as *fragilis*. Specimens identified as *fragilis* in the collections studied here were part of *Discodorididae coerulescens*, *Sebadoris fragilis*, *Tayuva lilacina*, *Peltodoris murrea*, *Asteronotus raripilosa*, and an unnamed, new species (*Discodorididae* sp. E). Specimens identified as *fragilis* in the literature are part of at least four distinct species, *Sebadoris fragilis*, *Tayuva lilacina*, and *Asteronotus raripilosa*. In collections studied here, several specimens identified as *concinna* and *nubilosa* actually were *fragilis*. In the literature, *fragilis* specimens have been designated under at least ten species epithets (placed in six different genera). The main reason why so many names have been used to designate *fragilis* is

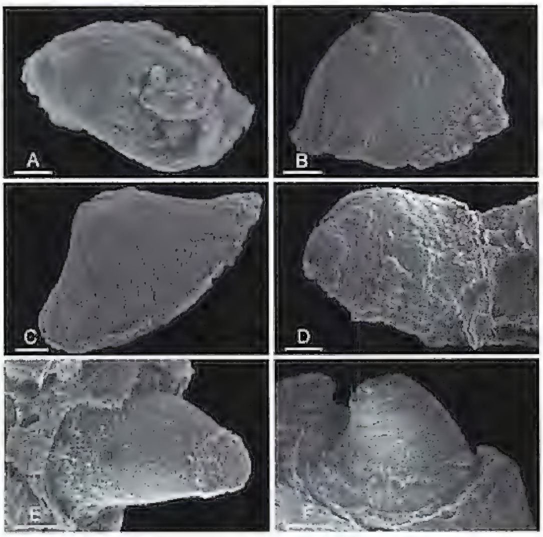

FIGURE 182. *Sebadoris fragilis*, penis. A. USNM 577550 (#2), scale = 40 µm.— B. USNM 577550 (#2), scale = 200 µm.— C. AM C126086, scale = 200 µm.— D. CASIZ 070011, scale = 200 µm.— E. CASIZ 073234 (#2), scale = 200 µm.— F. CASIZ 144022, scale = 200 µm.

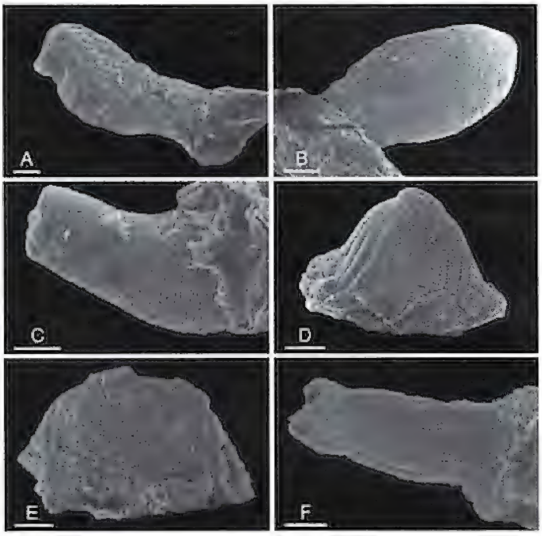

FIGURE 183. *Sebadoris fragilis*, penis. A. CASIZ 170083, scale = 100 µm.— B. CASIZ 099383, scale = 100 µm.— C. CASIZ 074075, scale = 100 µm.— D. CASIZ 168931, scale = 200 µm.— E. MV F79395, scale = 100 µm.— F. AM C418348, scale = 200 µm.

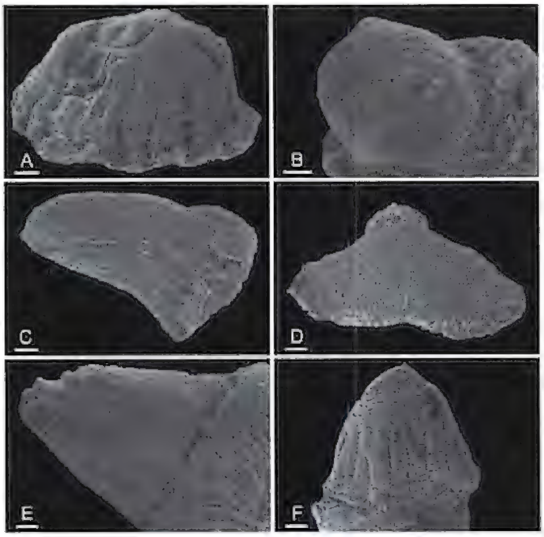

FIGURE 184. *Sebadoris fragilis*, penis. A. AM C133000, scale = 100 µm.— B. AM C418345 (#2), scale = 40 µm.— C. AM C418412, scale = 100 µm.— D. AM C164559, scale = 100 µm.— E. AM C418416 (#1), scale = 100 µm.— F. AM C418417, scale = 100 µm.

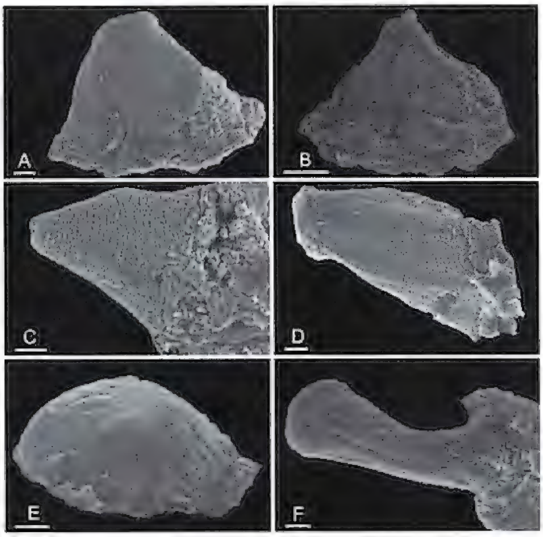

FIGURE 185. *Sebadoris fragilis*, penis. A. MV F86414 (#1), scale = 100 µm.— B. AM C416540 (#1), scale = 40 µm.— C. AM C416540 (#2), scale = 100 µm.— D. AM C164559, scale = 100 µm.— E. AM C418411 (#1), scale = 100 µm.— F. AM C147842 (#1), scale = 100 µm.

that its delineation and its infra-specific morphological variation have never been addressed. Edmunds (1971, 1972) attempted to distinguish *fragilis* from *concinna*, but his work was jeopardized by the fact that he regarded several published identifications as correct, although they are erroneous: for example, Kay and Young (1969) identified as *fragilis* specimens that are *Tayuva lilacina*. Thompson (1975) also attempted to distinguish *fragilis* from *concinna* but his views were jeopard-

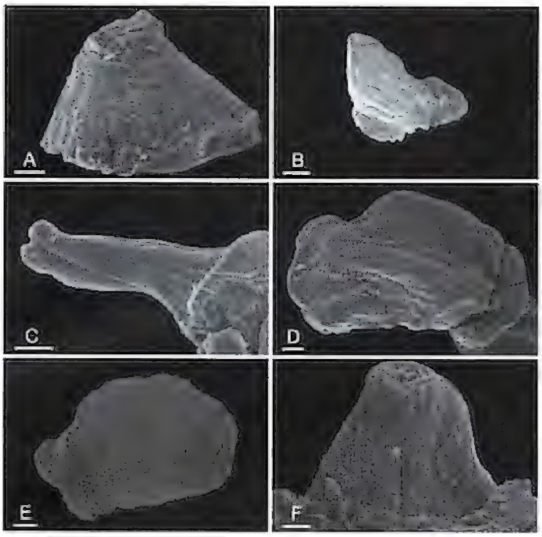

FIGURE 186. *Sebadoris fragilis*, penis. A. MNHN, Touho st. 1252 (#1), scale = 100 µm.— B. MNHN, Touho st. 1252 (#2), scale = 200 µm.— C. MNHN, Touho st. 1252 (#3), scale = 100 µm.— D. MNHN, Touho st. 1252 (#5), scale = 100 µm.— E. MNHN, Djibouti (#1), scale = 100 µm.— F. CASIZ073234 (#3), scale = 100 µm.

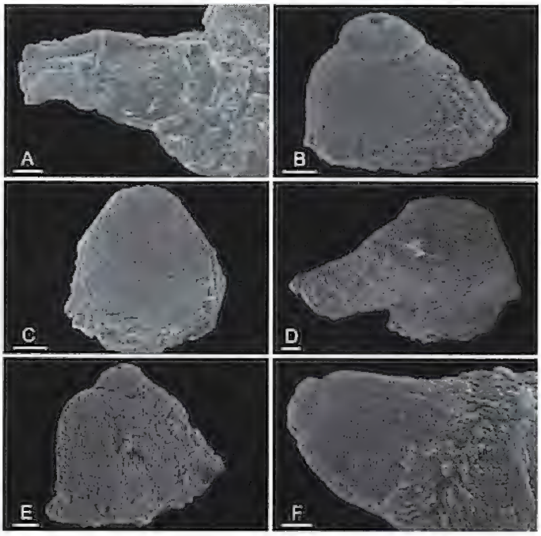

FIGURE 187. *Sebadoris fragilis*, penis. A. AM C099293, scale = 40 µm.— B. AM C415872 (#1), scale = 100 µm.— C. AM C415872 (#3), scale = 100 µm.— D. AM C415874, scale = 100 µm.— E. AM C418309 (#2), scale = 100 µm.— F. MCZ 048029, scale = 100 µm.

ized by the fact that the specimen he identified as *fragilis* was part of *Asteronotus raripilosa*. The dissection of 92 specimens (including the preparation of 38 radulae) offers for the first time a comprehensive understanding of *fragilis*. The present data show that: 1) all these specimens are part of a single species; and 2) the latter is easily distinguishable from other species, especially with features of the reproductive system, acknowledging that they may vary among individuals.

Here are a few comments on the synonymies proposed, based on the re-examination of all types available.

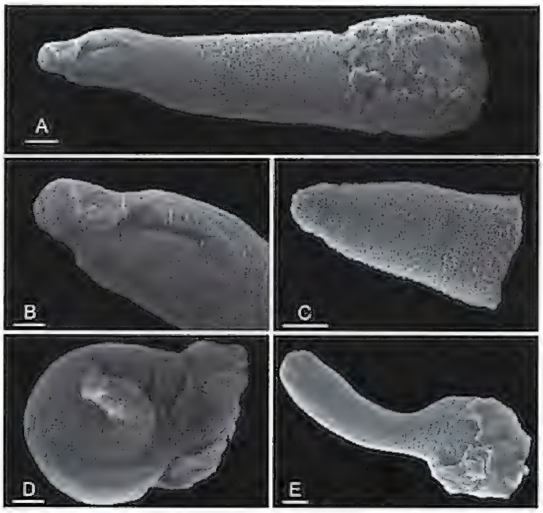

FIGURE 188. *Sebadoris fragilis*, penis. A. CASIZ 074193 (#2), scale = 100 µm.— B. CASIZ 074193 (#2), scale = 40 µm.— C. CASIZ 074193 (#1), scale = 100 µm.— D. CASIZ 074193 (#4), scale = 100 µm.— E. CASIZ 074193 (#5), scale = 100 µm.

The oldest name available is *Doris granulata*, which should have precedence over all other names. However, it is a case in which precedence can be reversed, i.e., *Doris granulata* is regarded here as a *nomen oblitum*, and *Sebadoris fragilis* is regarded as *nomen protectum* (*ICZN*, Article 23.9). Indeed, both *ICZN* Articles 23.9.1 and 23.9.2 apply: Bergh (1877b, 1878a) and O'Donoghue (1929) mentioned the presence of *Discodoris granulata* in the Red Sea based on Ehrenberg's contribution, but without adding new material and commenting on Ehrenberg's description, therefore, they did not really cite *granulata* as a valid species, but more as an available name from the Red Sea. Given that *fragilis* has remained a very common name for more than 100 years, prevailing usage is protected here.

The synonymy of *stragulata* with *fragilis* is new. Although the critical characters of the reproductive system could not be observed, the combination of the intestinal, ventral loop (only found so far in *nubilosa* and *fragilis*) and the tubercles that are not soft (*nubilosa* has soft, conical papillae) is sufficient to propose a synonymy of *stragulata* with *fragilis*. However, whether or not *stragulata* is a synonym of *fragilis* is not a crucial matter because the type locality of *stragulata* is unkown.

The synonymy of *hedleyi* with *fragilis* has never been proposed. The general organization of the reproductive system is characteristic of *fragilis*. O'Donoghue may have mentioned a penis armed with series of hooks and an independent hermaphroditic gland, although he did not really see them (the hermaphroditic gland for sure is *not* a discrete organ): either he wanted to support the classification of *hedleyi* within *Alloiodoris*; or he was convinced that these features would be present because he *hedleyi* was an *Alloiodoris*. Interestingly, the same problem was encountered with another *Alloiodoris* species, *A. nivosus* Burn, 1958: Burn (1962) mentioned the presence of a penial sheath internally covered with hooks in *Alloiodoris nivosus*; later, however, Burn (1969) finally regarded *nivosus* as a synonym of *Discodoris dubia* Bergh, 1904, and admitted that there were no hooks in the penial sheath (Dayrat 2006).

The synonymy of *vanikoro* with *fragilis* has never been proposed. This synonymy is supported by the presence of the diagnostic features of *fragilis* in the reproductive system of the holotype of *vanikoro*. Interestigly, Pruvot-Fol wrote that the latter had a shape similar to the shape of *stragulata*. This is not surprising given that both names are synonyms of *fragilis*. It is surprising, however, that Pruvot-Fol could create a new species name after she had pointed out that "the distinction among species [of *Discodoris*] is very often difficult and doubtful" (1934:67) and that *vanikoro* looked like *stragulata*.

Pruvot-Fol (1934) thought that the holotype of *sordidata*, which she transferred from *Doris* to *Discodoris*, was "probably" part of *fragilis*. This type really is part of *fragilis*, with which it shares several diagnostic features of the reproductive system. Note that *sordidata* Abraham, 1877 has no priority over *fragilis* Alder and Hancock, 1864. Bergh (1878a) tentatively transferred *sordidata* (as *sordida*) from *Doris* to *Platydoris*, with no explanation (and probably no reason). O'Donoghue (1929) followed Bergh's opinion and classified *sordidata* within *Argus*. It seems that the synonymy of *sordidata* with *fragilis* was never discussed again after Pruvot-Fol's (1934) contribution.

The dissection of one of the syntypes (the lectotype, designated here), demonstrates that the anatomy of *notiperda* cannot be distinguished from the anatomy of *fragilis*. It seems that *notiperda* is known only from the type material, and the synonymy between *notiperda* and *fragilis* has never been proposed.

The synonymy of *morphaea* with *fragilis* was proposed by Eliot (1909a) and then accepted by most authors (e.g., Eliot 1910a; Edmunds 1971, 1972; Rao and Kumary 1974; Thompson 1975). This synonymy likely is correct. Aside from the type, Bergh (1884a) described a second specimen (62 mm long, preserved) as *morphaea*, from the Philippines, which he found in the material of the Challenger Expedition. Eliot rightly suggested that this specimen also is part of *fragilis*. In particular, its reproductive system, carefully described by Bergh, is similar to the reproductive system of *fragilis*. Bergh (1884a:98) mentioned a 3 mm long praeputium, i.e., penial sac, with the opening of "the spermatic duct [lying] at the bottom of the cavity." Note that Bergh also carefully described the ventral loop of the intestine.

The species name *rubra* is not a synonym of *fragilis* because only the paralectotype of *rubra* is part of *fragilis*, and only the lectotype has a name-bearing function. However, the paralectotype is still part of the type material of *rubra*. The reproductive system could not be examined, but the combination of several features (e.g., color pattern, intestine with a ventral loop, tubercles not soft papillae) indicates that the paralectotype of *rubra* most likely is part of *fragilis*.

The name *Doris bellicosa* Kelaart, 1859 is a special case, because Alder and Hancock first used that name for the specimens they later named *fragilis*. The original description of *bellicosa* by Kelaart (1859) is extremely vague, and it was published again with no change many years later (Kelaart 1883). Eliot (1906b:666; 1906c:1004), who had access to color plates drawn by Kelaart, thought that *bellicosa* was "probably" a synonym of the *fragilis* of Alder and Hancock, but that there is "little resemblance between their plate and Kelaart's." It seems that *bellicosa* has not been cited since Eliot. The type of *bellicosa* could not be located, and that name should probably be regarded as a *nomen dubium*.

Two additional questions are discussed here: 1) whether or not non-type specimens previously identified as *fragilis* were part of *fragilis*; 2) which non-type specimens not identified as *fragilis* actually were part of *fragilis*. Accepting or rejecting previous identifications is jeopardized by the fact that descriptions often are incomplete. As a result, several identifications proposed in the literature remain ambiguous. Some of them have no real implications on our knowledge of the distribution of *fragilis* (e.g., *fragilis* is already known from the area), but several ambiguous identifications are potentially new records of *fragilis*.

For various reasons, no identifications from the literature could be confirmed with certainty. In most cases, the best that could be done was to say that specimens described in a publication were *not* part of some species, but it could rarely be determined with confidence that they actually were part of *fragilis* (or other species, for that matter). Also, a preserved specimen (CASIZ 082038) looked externally like preserved specimens of *fragilis*, but with a distinct penis, suggesting that, at this point, the only certain diagnostic features of *fragilis* are found in the reproductive system (see the section on diagnostic features). Therefore, one cannot exclude that specimens that externally seem to be part of *fragilis* could be part of other species. My intuition is that *fragilis* will also be distinguishable based on color pattern once we know more about the variation of the color of live animals, both in *fragilis* and in other species that look similar to it externally.

The specimens identified as *fragilis* by Eliot (1900) from Samoa probably are part of *fragilis*. However, this identification is uncertain because it is supported only by three features that may be misleading: animals "brownish green, mottled with darker shades of the same color, the foot and under surface of the mantle being similarly marked;" the size of live animals from 50 to 85 mm long; and the "extraordinary powers of self-mutilation," although a loss of a complete ring of lateral notum, observed in one specimen (CASIZ 144022), does not seem to have been mentioned in other species.

Eliot (1909a) identified two specimens (75 mm long, preserved) as *fragilis*, from Colombo, Sri Lanka. Several characters mentioned by Eliot are compatible with *fragilis* but are not diagnostic of it, such as a wide bursa copulatrix (spermatheca) and a small receptaculum seminis (spermatocyst), the intestine with a ventral loop, and the radular formula —45 × (75-0-75). Indeed, *nubilosa* also has a long, convoluted intestine with a ventral loop. However, it is possible that Eliot did not examine specimens of *nubilosa* because he described "hard" tubercles on the dorsal notum (whereas *nubilosa* bears long, conical, soft papillae that are distinguishable). Also, Eliot (1906c), who reexamined the type material of *fragilis*, stated that the tubercles of the Sri Lanka specimen were similar to the tubercles of the type material of *fragilis*. Eliot's description of the praeputium "with folds and knots, but no armature," is puzzling. However, Eliot's identification is accepted as a record of *fragilis* because, so far, an intestine with a long ventral loop is only known in *nubilosa* and *fragilis*.

The 90 mm long preserved specimen identified as *fragilis* by Eliot (1910a) from the Chagos Archipelago probably was part of *fragilis*. Indeed, Eliot (1910a) described a feature that, so far, was observed only in *fragilis* (not in all specimens): the dorsal mantle is made of two layers that separate easily, a thin, external layer and a thick, muscular, internal layer, which is especially striking on the dorsal surface of the body cavity. This peculiar structure of the mantle was not observed in other species with a dark brown dorsal notum, such as *Asteronotus raripilosa*. Also, Eliot described several characters that are compatible with *fragilis*, such as a radular formula 56 × 90/100-0-90/100, the presence of a long intestine with a ventral loop, a wide bursa copulatrix (spermatheca) and a small receptaculum seminis (spermatocyst). Note, however, that Eliot (1910a) did not describe the penis, probably because it was small and unarmed.

Edmunds (1971) described eight specimens as *fragilis* from Oysterbay, Dar es Salaam, Tanzania. The small, conical penis that he represented is one of the diagnostic features of *fragilis* and suggests that he examined specimens of *fragilis*. The diagnostic loop of the fertilization duct can only be inferred from Edmunds's (1971: fig. 4C) schematic drawing. Also, according to this drawing, the bursa copulatrix is not much larger than the receptaculum seminis, which has to do with the schematic nature of Edmunds's representation of the reproductive system. Edmunds's general opinion on the identification of *fragilis*, especially the use of the dorsal color, was jeopardized by the fact that he thought that Kay and Young's (1969) specimens of *fragilis* from Hawaii were part of *fragilis*. Also, the potentially good taxonomic characters (e.g., white rhinophoral tip, shape of labial cuticle, shape of radular teeth) that he proposed actually are of little help (if any) for identifying *fragilis*.

Edmunds (1972) identified three specimens (one from Tanzania and two from the Seychelles) as *fragilis*, and he briefly mentioned that their anatomy was similar to the specimens he had described from Tanzania (Edmunds 1971). These three specimens are not part of *Tayuva lilacina* because of the number of teeth per half row (56 teeth in a 50 mm long specimen, probably alive, and 60 teeth in a 52 mm long specimen, probably alive). The presence of large, dark blotches on the ventral surface also is incompatible with *lilacina*. Although Edmunds did not describe the diagnostic features of *fragilis* (i.e., the reproductive system) in those specimens, it seems unlikely that he confused *fragilis* with other species with a similar, dark brown color pattern, such as *Asteronotus raripilosa* or *Sebadoris nubilosa*. Indeed, Edmunds (1971) had identified correctly both *nubilosa* and *fragilis*, and *raripilosa* has diagnostic characters in the reproductive system that Edmunds could not have missed.

Rao and Kumary (1974) described in great detail multiple specimens of *fragilis* from southeastern India. Their drawing of the reproductive system (Rao and Kumary 1974: fig. 2) is exactly the same as the drawings presented here, except for the diagnostic fertilization loop that the authors overlooked. Also, the black-and-white picture of the animal that they published represents the commonest color pattern of *fragilis*.

The photograph of the specimen identified as *fragilis* by Orr (1981) from Hong Kong is unclear. However, the radular formula of 30 × (58-0-58), not compatible with *lilacina*, in which there are maximum 40 teeth per half row, indicates that Orr probably observed a specimen of *fragilis*. The 75 mm long specimen identified as *fragilis* by Tan et al. (1987) from Taiwan could be part of *fragilis*. However, this interpretation, based only on the ventral color pattern and the size, remains uncertain. The 80 mm long specimen identified as *fragilis* from Coral Bay, Western Australia, by Wells and Bryce (1993), the three specimens (80 mm maximum length, alive) identified as *fragilis* by Marshall and Willan (1999) from Heron Island, Great Barrier Reef, and the specimen identified as *fragilis* by Coleman (2001) from Tryon Island, Queensland, all represent the commonest dorsal color found in *fragilis*.

White (1948) identified with "difficulty" a 54 mm long preserved specimen from Ceylon as *fragilis*, but the few characters that she provided do not help establish whether she saw *fragilis* or any other species. The presence of "longer papillae, probably branched but too much retracted for details to be made out" and a gill pocket with "six lobes" suggests that White actually saw specimens of *raripilosa* Abraham, 1877, a species for which she created the name, *Otinodoris winckworthi* White, 1948, on the same page of the same contribution… Edmunds (1971) thought that this specimen could be part of *Sebadoris nubilosa*, which seems unlikely (because of the presence of a six-lobed branchial sheath). However, the absence of radula is puzzling.

Thompson identified a 120 mm long specimen as *fragilis* from Heron Island, Great Barrier Reef. Several features described by Thompson indicate that he did not examine *fragilis*, in particular the "broad rather flattened, curved oral tentacles," the branchial sheath "divided into six valve-like crenulations," and the 6 mm long penis. Thompson (1975) argued that all previous authors had overlooked the crenulation of the branchial sheath as a principal difference between *concinna* and *fragilis*. Authors have not overlooked anything: *fragilis* does not have a six-lobed branchial sheath. The specimen identified as *fragilis* by Thompson likely is part of *raripilosa*. The presence of a six-lobed branchial sheath indicates that this specimen could be part of *Asteronotus cespitosus*, *Asteronotus raripilosa*, or any *Platydoris* species. Given that it is obviously not part of a *Platydoris* species or *Asteronotus cespitosus*, it should be part of *Asteronotus raripilosa*. However, the smooth, tapering, and slightly hook-shaped penis described by Thompson is hardly compatible with the strongly armed penis of *raripilosa*. Therefore, the interpretation proposed here is largely tentative. In any case, Thompson's use of the name *fragilis* was a misidentification. Marshall and Willan (1999), who collected and described many nudibranchs from Heron Island, thought that Thompson's identification was correct. Also, Ortea and co-authors (1981) pointed out that Thompson's identification was problematic, but their comment on Thompson's work was confused by the fact that they used *fragilis* for at least two different taxa (*Sebadoris fragilis* and *Tayuva lilacina*).

All the specimens that have been identified as *fragilis* from Hawaii (Kay and Young 1969; Kay 1979; Bertsch and Johnson 1981) are part of *lilacina* (see this species). Based on these identifications, several authors (e.g., Edmunds 1971, 1972; Ortea et al. 1981; Gosliner 1987) have stated that *fragilis* was present in Hawaii. Edmunds (1971, 1972), who noticed that the Hawaiian specimens were different from the specimens of *fragilis* found elsewhere, thought that these specimens should still be part of *fragilis* because "*concinna* [had] not been reported from this area." The reality is the opposite: the Hawaiian specimens of *fragilis* are smaller because they are *not* part of *fragilis*; instead, they are part of *lilacina*, which Edmunds probably referred to as *concinna*. There is a chance that *fragilis* really is in Hawaii, but this presence has not been positively demonstrated.

The specimen from Queensland identified as *fragilis* by Willan and Coleman (1984:36, fig. 112) is part of *Peltodoris murrea*. The record of *fragilis* from South Africa (Gosliner 1987) is a record of *Tayuva lilacina* (see this species). Records of *fragilis* from the Canary Islands (Ortea et al. 1981; Gosliner 1987; Wirtz 1995; Costello et al. 2001) are most likely records of *Tayuva lilacina* (see this species). Ortea and co-authors (1981) thought that the specimen identified as *Discodoris* sp. by Pruvot-Fol (1953), from the coasts of Senegal, could be part of *fragilis*. This specimen may belong to *Tayuva*, but nothing indicates that it may be part of *fragilis*. Note that Wirtz (1995) mentioned that *fragilis* was present in Senegal, based on Ortea and co-authors's contribution.

In the present study, the species name *concinna* is regarded as a *nomen dubium* (see *concinna*). Below, only are mentione the specimens identified as *concinna* that could be part of *fragilis* (see *concinna* for other cases).

Eliot (1909a) identified a 26 mm long, preserved specimen as *concinna* from Trincomalee, Sri Lanka. The color potentially is compatible with several species: "it was brownish gray when alive, with darker patches. Down the centre of the back ran a line of not clear whitish areas; on either side of this was a line of dark patches more deeply coloured than the rest. There were numerous other patches, smaller and fainter." However, the radular formula of 20 × (60-0-60) is hardly compatible with *lilacina*. Also, the fact that this specimen was "probably immature" indicates that it might have been a young specimen of *fragilis*, because 26 mm long specimens of *lilacina* are fully mature, whereas specimens of *fragilis* measuring less than 30 mm in length are not mature.

Vayssière (1912) identified several specimens as *concinna* from Djibouti. Some of the specimens reexamined here from Djibouti (MNHN) likely are some of the specimens that Vayssière described (same locality and same collector). The color (dark blotches of various sizes and shapes upon a yellowish dorsal background, and presence of a dark ring on the hyponotum, adjacent to the foot), the size (from 50 to 80 mm in length, preserved), and a radular formula of 24 × (70-0-70) in one of the large specimens indicate that the specimens described as *concinna* by Vayssière were part of *fragilis*.

Baba (1933) described one 80 mm long specimen, alive, from Tomioka Bay, Amakusa (~32°N), which he identified as *concinna*. This specimen likely is part of *fragilis*: the black-and-white drawing of the dorsal surface fits with *fragilis* variation, as well as the radular formula 45 × (55-0-55).

Gohar and Soliman (1967) described multiple specimens (maximum 150 mm long in length, alive) as *concinna* from the Red Sea. Many features indicate that they examined specimens of *fragilis*, such as the color, which is the commonest color pattern of *fragilis*, the radular formula and the teeth shape. Unfortunately, Gohar and Soliman did not describe the intestine. Also, their illustration of the reproductive system is fully compatible with the reproductive system of *fragilis* (e.g., bent receptaculum seminis, bursa copulatrix much larger than the receptaculum seminis), but does not clearly represent the diagnostic features of *fragilis* (i.e., the conical penis, and the convoluted fertilization duct). Also, Gohar and Soliman vaguely described a "large penis" (it is unclear whether or not they refer to the penis when he mentions a "genital papilla" of 5 mm in diameter). Soliman (1983) described again some specimens of *concinna* from the Red Sea. Those specimens are identical to the specimens he had described with Gohar.

The specimen identified as *concinna* by Willan and Coleman (1984) from Queensland, has a less typical color pattern than the specimen that they identified as *fragilis* in the same publication. However, the dark overall appearance (with multiple small dark pigments) indicates that it should be *fragilis* rather than *lilacina*. The 95 mm long specimen identified as *concinna* by Guangyu (1986) from the South China Sea probably is part of *fragilis*. However, this interpretation, based only on the dorsal color pattern and the size, remains uncertain. The 50 mm long specimen identified as *concinna* by Coleman (1989) from Tryon Island, Great Barrier Reef, should be part of *fragilis*. The 60 mm long specimen identified as *concinna* by Wells and Bryce (1993) also has a less typical color than the specimen that they identified as *fragilis* in the same publication. However, the dark overall appearance (with multiple small dark pigments) and the size indicate that it should be *fragilis* rather than *lilacina*. Finally, the specimens that Terry Gosliner and I referred to as *concinna* are all designated here as *fragilis* (Dayrat and Gosliner 2005). Back then, the present study was not completed yet, and the name *concinna* was selected by default.

Baba (1949, 1955) identified seven specimens (length up to 80 mm) as *concinna* from Sagami Bay, Pacific coasts of Japan. Several features described by Baba indicate that he probably examined specimens of *fragilis*: a "ashy brown" ground color of the dorsal notum "overlaid with dark brown mottles of varying intensity, the darkest being on each side of the middle line, as a series of large oval markings of almost black;" a "ashy brown" underside of the body "irregularly spotted with dark brown;" a radular formula of 45 × 55-0-55; and a 80 mm maximum length (probably alive). However, this interpretation is uncertain. In particular, Baba's description also is compatible with the specimen CASIZ 082038, also from Sagami Bay, externally similar to *fragilis* (although only the preserved color of CASIZ 082038 is known) but distinct from it internally. Therefore, one cannot exclude that Baba designated as *concinna* specimens that were part of different entities. The picture of the *concinna* specimens by Okutani (2000) may illustrate a *fragilis* specimen (see *concinna*).

Eliot's (1913) vague description of three specimens (41 mm maximum length, preserved) as *concinna* is compatible with several species, including *lilacina* and *fragilis*. However, there is a better chance that they might be part of *lilacina* than *fragilis* but this remains largely speculative. The specimen identified as *concinna* by Lim and Chou (1970) could be part of *fragilis* or *Asteronotus raripilosa*. Thompson (1975) described two 30 and 65 mm long specimens, alive, identified as *concinna*. The dorsal and ventral colors, the radular formula of 32 × (57-0-57), and the fact that specimens were immature indicates that: 1) they could not be part of *Tayuva lilacina*, and 2) they could be part of *fragilis*. However, Thompson mentioned the presence of five and eight gills, which is unexpected for *fragilis*.

The 60 mm long specimen identified as *noumeae* by Risbec (1956) from Nhatrang, Vietnam, probably is part of *fragilis*. Note that Risbec (1956) referred to several specimens of *noumeae* but dissected only one of them. These specimens, not in the MNHN collections, may still be in Nhatrang, where there might be some old collections of marine invertebrates. Although Risbec published several drawings, his description is largely incomplete and doubtful: for example, his illustrations of the reproductive system are helpless, and his description of the radula is questionable (35 teeth per half row). However, the combination of a few features indicates that Risbec may have observed specimens of *fragilis*: the tubercles that are not soft *nubilosa*-like papillae, the intestine with a long, ventral loop, and the large caecum of the stomach. Therefore, there is a great chance that Risbec described two series of specimens from the same localities (Nhatrang) under two different species names: *Discodoris notiperda* and *Peltodoris noumeae*. This can be explained by the fact that Risbec dissected only one specimen for each series (he states that he dissected only specimen for *Peltodoris noumeae*, and only one syntype of the type series of *Discodoris notiperda* was dissected). This should not surprise the reader: Risbec is certainly not famous for the accuracy of his taxonomic identifications and anatomical descriptions (although he is not the only one).

Several authors (Eliot 1906b, 1906c, 1909a, 1910a; O'Donoghue 1929; Edmunds 1971, 1972) have regarded *concinniformis* as a synonym of *concinna*. Considering that some non-type specimens of *concinna* are part of *fragilis*, it is worth asking whether or not some specimens of *concinniformis* are part of *fragilis* too. Bergh (1888, 1890, 1905) described a total of five specimens of *concinniformis*, including a variety: two from Mauritius (type locality), two from Amboina, and one from Nusa Bei Reef, on the northwestern coasts of Timor. These specimens are probably not part of *lilacina* (their radular formulae are not compatible with the variation found in *lilacina*). However, there is no positive indication that they are part of *fragilis*, because Bergh's descriptions are too vague and because the type material is not informative (see *concinniformis*). However, the specimen described by Bergh as a variety of *concinniformis* is regarded here as part of *fragilis* (the holotype of that variety has a notum with fragile edges, as in *fragilis*).

Finally, the 60 mm long specimen identified as *Discodoris* sp. by Coleman (2001) from Western Australia could be part of *fragilis*, although a dissection would be necessary to confirm this interpretation. The specimen identified as *Platydoris speciosa* by Okutani (2000:792, fig. 3a) should also be part of *fragilis* (it is unclear whether his figures 3a and 3b are from the same animal). In any case, it is clearly different from *Platydoris ellioti*, regarded by Dorgan et al. (2002) as the valid name for *Platydoris speciosa* (see *ellioti*).

SUPRA-SPECIFIC RELATIONSHIPS.— Supra-relationships between *fragilis* and other discodorid species have been rarely discussed. According to Eliot (1909a), *concinna* "appears to be nearly related to *D. notha* from the West Indies." There are two possible explanations for this statement: one is simple, and the other is much more complicated. First is the complicated explanation. Prior to the present study, the type material of *notha* would include four syntypes: two of them clearly belong to *Discodorididae branneri* (*Discodoris evelinae* and *Discodoris hedgpethi* are synonyms) because they have a strong penis entirely covered with spines (see *branneri*); the two other specimens, which lack this typical penis, may be part of *hummelincki*. This interpretation, however, is uncertain because it is only supported by the fact that a structure described and drawn by Bergh could be similar to the muscular wall found around the distal area of the reproductive system in all *Tayuva*. Although Eliot's use of the name *concinna* could mean '*lilacina*,' it is unlikely that Eliot thought that *concinna* could be close to *notha* because of this particular detail in the reproductive system because, it seems that he never mentioned it, which means that he certainly did not see it. Eliot's statement can be easily explained by the fact that, according to the original description, *notha* also have a light ground color bearing darker patches on the dorsal notum. However, this color was already known in many other species, such as *Discodorididae branneri*, *Discodoriidae voniheringi*, and *Discodorididae muta*. Even the simplest explanation does not explain Eliot's decision of comparing *concinna* only with *notha*.

In any case, a phylogenetic test of the relationships of *fragilis* shows that *fragilis* does not belong to *Discodoris*. It belongs to *Sebadoris*, a clade that includes *nubilosa*, the type species of *Sebadoris* under the *ICZN*, and *fragilis*. The Linnaean binomial for *fragilis* should be *Sebadoris fragilis*, which also is a possible name under the *ICPN*. Note that, overall, if one considers *fragilis* and all its synonyms and misidentifications, *fragilis* was classified within six genera (*Alloiodoris*, *Argus*, *Discodoris*, *Doris*, *Peltodoris*, and *Platydoris*), although none of those affinities were tested through a phylogenetic analysis.

FUTURE STUDIES.— Any morphospecies can potentially include several cryptic species. The study of individual variation and its geographic distribution may help discover cryptic species. Morphologically, *fragilis* is a homogeneous species. However, several specimens from the Seychelles (CASIZ 074193) had a penis that differed from other specimens (though those differences could be individual variants). In the future, however, one may want to test with non-morphological data whether or not all populations of *fragilis* are part of a single species.

Asteronotus Ehrenberg, 1831

Under the *ICZN*, *Asteronotus* is a taxon of genus-level. Type-species: *Asteronotus hemprichi* Ehrenberg, 1831, by monotypy, which is regarded as a synonym of *Asteronotus cespitosus* (Hasselt, 1824).

The phylogenetic diagnosis of *Asteronotus* includes four classes of characters, depending on their phylogenetic significance. 1) One synapomorphy exclusively found in this taxon: lateral teeth with a high base, which gives them a convex (instead of concave) appearance (especially striking in the innermost teeth); only this synapomorophy can be regarded as diagnostic of *Asteronotus* (i.e., only this character can be used to identify that a species belongs to *Asteronotus*). 2) Four synapomorphies of *Discodorididae*: a notched upper lip of the bilabiate anterior foot, digitiform or conical oral tentacles that are *not* expansions of the lateral mouth lips, a flattened prostate divided in two parts of distinct color, and two blood glands. 3) Characters found in many other dorid nudibranchs, e.g., absence of rachidian teeth, hamate lateral teeth, etc. 4) Characters found in other discodorids, although their exact phylogenetic significance is still unknown, e.g., the presence of an accessory gland with a hollow spine.

In the present contribution, *Asteronotus* refers to a clade name, but is not assigned to any particular rank. Under the *ICPN*, *Asteronotus* is a converted clade name: it remains an informal clade name until it is phylogenetically defined *and* formally registered. *Asteronotus* could be phylogenetically defined through an apomorphy-based definition as "the clade stemming from the first organism or species to possess lateral teeth with a high base, which gives them a convex (instead of concave) appearance (especially striking in the innermost teeth), as inherited by *Asteronotus cespitosus* (Hasselt, 1824)."

Asteronotus raripilosa (Abraham, 1877) New combination

Figures 189-204.

Doris raripilosa Abraham, 1877:257, plate XXIX, figs 29-30.
Discodoris ? *raripilosa*.— Bergh, 1878a: XXXIV.— Bergh, 1880a:47.— Bergh, 1884a:93.
Discodoris raripilosa.— Rochebrune, 1882a:50.— Risbec, 1956:15.
Hoplodoris desmoparypha Bergh, 1880a:51-56, plate C, figs 5-9, plate F, figs 1-18.— Bergh, 1905:113-115, plate XIV, figs 41-46, plate XV, figs 1-2.— White, 1950:100.— Narayanan, 1968:202, figs 10a-c. **New synonym.**
Platydoris papillata Eliot, 1903:379-380.— Eliot, 1906b:648-649.— Eliot, 1910a:425.— Dorgan et al., 2002:312. **New synonym.**
Discodoris nubilosa.— Allan, 1947:455-456, plate XIII, figs 17-21 [not *nubilosa* Pease, 1871].
Otinodoris winckworthi White, 1948:203-205, figs 6-11.— Valdés, 2004b:49-53, figs 1A-2. **New synonym.**
Otinodoris sp. Coleman, 2001:66, unnumbered figure.— Valdés, 2002:604-607, figs 34B, 39-41.
Otinodoris sp. 1. Marshall and Willan, 1999:80, 174, 223, figs 139-140.
Sebadoris sp. Debelius, 1996:248, unnumbered figure.— Ono, 1999:109, fig. 177.
Doridacea sp. 3. Ono, 1999:138, fig. 230.
Sebadoris sp. cf. *nubilosa* Ono 2004:146, fig. 295.

Type material (*raripilosa*).— Holotype (NHM 1852.10.7.6), by monotypy: one specimen 70/45 mm preserved, leg. Zoological Society, [no date].

Type material (*desmoparypha*).— The two syntypes could not be found and are probably lost.

Type material (*papillata*).— The nine syntypes could not be found and are probably lost.

Type material (*winckworthi*).— The holotype, the only specimen known for *winckworthi*, could not be found. It is not at the Natural History Museum, London. My requests to the Colombo Museum, Sri Lanka, remained unanswered. It is probably lost.

Type locality (*raripilosa*).— No locality was indicated, neither on the label nor in the original publication. However, the specimen was probably collected from the tropical Indo-West Pacific, as most of the species described by Abraham (1877).

Type locality (*desmoparypha*).— Palau, western Pacific Ocean.

Type locality (*papillata*).— Chuaka, eastern coasts of Zanzibar, Indian Ocean.

Type locality (*winckworthi*).— Ceylon Pearl Banks, Indian Ocean.

Type material condition (*raripilosa*).— The holotype is globally well preserved, although the central part of the dorsal notum, smooth and thin, was damaged by more than one century of preservation. The buccal mass was removed prior to the present study and is probably lost.

Additional material dissected.— **Madagascar**, Ile Sainte Marie, off Soanambo Hotel, 5 April 1990, one specimen 155/90 mm preserved, leg. Hank Chaney, identified as *Otinodoris* sp. by A. Valdés (CASIZ 073238) [this specimen was dissected by Valdés (2002) prior to the present study; the picture provided by Valdés (2002, fig. 34C) is actually a picture of another specimen, CASIZ 099347]; **Tanzania**, Mtwara Region, Manahuanja Island, 1 November 1994, one specimen 65/55 mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 099347) [a color picture of this specimen was published by Valdés (2002, fig. 34B) under an incorrect catalogue number 'CASIZ 073238']; **Indian Ocean**, Mascarene Islands, Mauritius, 13 October 1873, one specimen 85/55 mm preserved, leg. N. Pike, identified as *Discodor-*

ididae by an unknown identifier (MCZ 004575); **Australia**, Queensland, Low Isles, [no date], one specimen 80/55 mm, [leg. unknown], identified *Discodoris fragilis* by Robert Burn [but the name *Sebadoris nubilosa* was also written on a separate label by an unknown identifier] (NMV F16748); **Papua New Guinea**, Palau, Ngermutideck Island, Ngermutideck, 20 September 1996, three specimens 75/45 (#2), 65/45 (#1) and 45/25 (#3) mm preserved, leg. Larry Sharon, identified as *Discodoris* by T. M. Gosliner (CASIZ 109748); **Philippines**, [no collecting date], one specimen 100/65 mm preserved, leg. Semper, not identified (ZMUC, no catalogue number); **Japan**, Ryukyu Islands, Okinawa, 1.3 km ENE of Maeki-zaki, Seragaki Beach, 26°30.4′N, 127°52.6′E, 30 feet maximum depth, 25 February 1989, one specimen 80/65 mm preserved, leg. R.F. Bolland, identified as *Discodoris* by T. M. Gosliner (CASIZ 070066).

DISTRIBUTION.— Tropical Indo-West-Pacific. The present study provides records of *raripilosa* from several regions: Madagascar, Tanzania, Mauritius, Papua New Guinea, Australia (Queensland), Philippines, and Japan. Some of these localities have been mentioned in the literature, but under other names than *raripilosa*: as *Hoplodoris desmoparypha* in Palau (Bergh 1880a; type locality of *desmoparypha*) and Sangihe Island, Indonesia (Bergh 1905); as *Platydoris papillata* in Zanzibar (Eliot 1903; type locality of *papillata*) and southern India (Eliot 1906b); as *Otinodoris winckworthi* in Ceylon (White 1948; type locality of *winckworthi*); as *Otinodoris* sp. in Madagascar (Valdés 2002) and Heron Island, Queensland (Marshall and Willan 1999; Coleman 2001); as *Sebadoris* sp. from Java (Debelius 1996) and Zamami Island, Japan (Ono 1999); as *Sebadoris* sp. cf. *nubilosa* from southern Japan (Ono 2004); and possibly as Doridacea sp. 3 in Agenashiku Island, Japan (Ono 1999).

Other records are problematic. Rochebrune (1882a) simply mentioned a single specimen of *Discodoris raripilosa* collected by Dr. Harmand from Poulo-Condor, Philippines; however, Rochebrune did not provide any morphological or anatomical information and his identification remains uncertain, although *raripilosa* is present in the Philippines. Allan (1947) identified a specimen as *Discodoris nubilosa* which most likely is part of *raripilosa* because of the presence of branched papillae on the dorsal notum (see discussion). The locality where this specimen was collected, Angurie Pool, at the northern border of the New South Wales, Australia, would then be the southernmost record for *raripilosa*. White (1950) briefly commented on the anatomy of *desmoparypha* based on specimens collected from Zanzibar. However, her description was incomplete: she might have looked at *desmoparypha*, but that is uncertain. Finally, Narayanan (1968) described three specimens from the Gulf of Kutch, off western coasts of India, which could be part of *raripilosa* (as *Hoplodoris desmoparypha*). However, his description is brief, and he does not mention the branched dorsal papillae, nor does he mention the lobed branchial opening (although the presence of flat, oral tentacles suggests that he actually saw *raripilosa*).

OCCURENCE.— Seven new specimens were dissected here. Allan (1947) mentions one specimen, Ono (1999) at least two, Debelius (1996) one, Marshall and Willan (1999) two –of which one was probably examined here, and Coleman (2001) illustrated one of Julie Marshall's specimens. In addition to those 13 specimens, one must add the two holotypes and possibly two other specimens (Rochebrune 1882a; Ono 1999). Marshall and Willan considered *raripilosa* as rare, which might be true, especially because it can hardly be missed given its large adult size. However, some specimens were collected at night (Marshall and Willan 1999), which might explain why so few specimens are known.

HABITAT.— Reef flat (CASIZ 109748), sand flat (NMV F16748), on strewn coral rubble (CASIZ 070066), on coral substrates, on top of platform in shallow water (Marshall and Willan 1999).

LITERATURE.— Most authors have provided some information about the color and the morphology of the dorsal notum (Bergh 1880a, 1905; Eliot 1903, 1906b; Allan 1947; White 1948, 1950; Valdés 2002; Debelius 1996; Marshall and Willan 1999; Ono 1999, 2004; Coleman 2001).

In particular, the last six publications include color pictures of live animals. Several authors also provided some information about the radula (Bergh 1880a, 1905; Eliot 1903, 1906b; Allan 1947; White 1948, 1950; Valdés 2002). Bergh (1880a, 1905) and Eliot (1903, 1906b) provided accurate descriptions of the reproductive system. However, the illustrations of the reproductive system published by White (1948, 1950) and Valdés (2002) are erroneous (see discussion). Bergh (1878a, 1880a, 1884a), Rochebrune (1882a) and Risbec (1956) used the combination *Discodoris raripilosa*, without discussing any anatomical or morphological information. Finally, note that some discussions about *Hoplodoris desmoparypha* can also be found in Gosliner and Behrens (1998), Miller (1991), Valdés (2002), and Fahey and Gosliner (2003).

Remarks on the original description (*raripilosa*, Figs. 189A, 190A-B).— Abraham described the color of the preserved animal as "dirty brown above, thickly mottled with brownish black on the sides and around the border; the branchiae are light reddish brown; underneath, the general tint is reddish brown…" After 130 years in alcohol, the specimen is dirty grayish. Abraham rightly distinguishes the tubercles from the papillae on the dorsal surface of the notum. He did not point out that the papillae are branched because only a few of them are branched. Also, he mentioned a few important characters that have often been overlooked, such as the flat oral tentacles, "semicrescentic in outline," and the lobate branchial sheath. The number of rhinophoral lamellae could not be determined. Abraham did not mention whether or not the labial cuticle was armed with jaws. This character could not be verified. The reproductive system, still in place, could be examined. It was not drawn though, because it would have required destroying some structures. However, an accessory gland with a coiled spine and an armed penis were found, exactly identical to the ones found in the additional, non-type specimens.

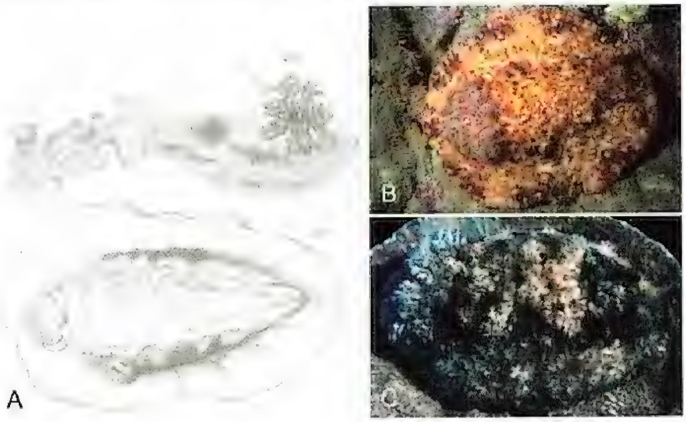

Figure 189. *Asteronotus raripilosa*, dorsal color. A. Dorsal and lateral views from the original description of *Doris raripilosa* (Abraham 1877: plate XXIX, figs 29-30.— B. CASIZ 099347 (T. M. Gosliner).— C. Dorsal color, CASIZ 073238 (H. Chaney).

Remarks on the original description (*desmoparypha*, Figs. 190C-G).— The original description of *desmoparypha* is detailed and largely accurate. In particular, Bergh's drawings (1880a, plate F, figs 5-15, plate C, figs 7-9) of the different parts of the reproductive system speak for themselves: the shape and the position of the spine of the accessory vestibular gland are described carefully. Bergh did not mention branched papillae *per se*, but this can be explained easily by the fact that preserved specimens may have just a few dorsal branched papillae (see below). Jaws are present on the labial cuticle, which Bergh (1905) confirmed in new specimens.

Remarks on the original description (*papillata*).— Eliot provided accurate and detailed information about the color of the dorsal notum, and the external morphology (e.g., lobate gill-pocket). Eliot mentioned the presence of an accessory gland but no "hasta" (i.e., spine). However, a few years later, Eliot (1906b) corrected his observations and mentioned the presence of a spine in the accessory gland. Eliot specifically mentioned that he did not find jaws. This could be explained by the fact that jaw plates are small compared to the size of the labial cuticle, and they could easily be overlooked. In fact, it took quite some time to find them in several specimens. The original description of *papillata* is also interesting because Eliot thoroughly compared his specimens with *Asteronotus* and *Platydoris* species (see discussion).

Remarks on the original description (*winckworthi*, Figs. 190H-J).— The original description of *winckworthi* provides accurate information about the external morphology (i.e., presence of branched papillae, ear-shaped oral tentacles, crenulate branchial sheath) and the radular teeth. White did not mention whether or not *winckworthi* had an armed labial cuticle. The description of the reproductive system can hardly be used for comparison because of several confusions: only one spermatic pouch (instead of two, as always) is mentioned; the prostate has probably been misinterpreted as the hermaphroditic gland (which White erroneously thought was independent from the digestive gland). The specimen dissected by White was probably immature sexually. Creating a new genus name and a new species name for it was probably unwise. The lack of any mention of an accessory vestibular gland (observed in all specimens that belong to this species) can be explained by the fact that White did not properly describe the reproductive system.

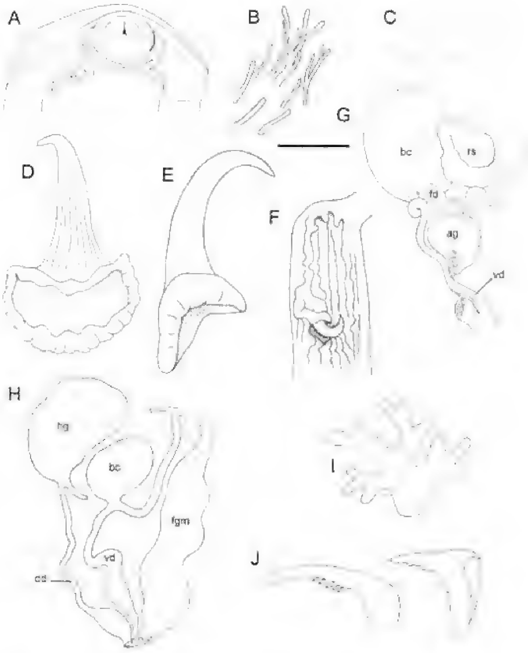

Figure 190. *Asteronotus raripilosa*, holotype, NHM 1852.10.7.6, and illustrations from original descriptions (except for D). A. Anterior, ventral view, holotype, total width = 40 mm.— B. Dorsal, fragile, branched papillae, holotype, scale = 10 mm.— C. Oral tentacle, *Hoplodoris desmoparypha*, after Bergh (1880a: plate F, fig. 17).— D. Hollow spine of accessory gland, *Hoplodoris desmoparypha*, after Bergh (1905: plate 15, fig. 2).— E. Hollow spine of accessory gland, *Hoplodoris desmoparypha*, after Bergh (1880a: plate F, fig. 12).— F. Vestibule opened, with tip of hollow spine, *Hoplodoris desmoparypha*, after Bergh (1880a: plate F, fig. 11).— G. Spermatic pouches and accessory gland, *Hoplodoris desmoparypha*, after Bergh (1880a: plate F, fig. 5).— H. Reproductive system, *Otinodoris winckworthi*, after White (1948: fig. 9).— I. Dorsal, branched papilla, *Otinodoris winckworthi*, after White (1948: fig. 7).— J. Lateral, radular teeth, *Otinodoris winckworthi*, after White (1948: fig. 11).

Description of new specimens (Figs. 191-204).— *Color*: The ground color of the dorsal notum is whitish (e.g., CASIZ 070066), yellowish (e.g., CASIZ 099347) or brown (e.g., CASIZ 073238) and bears many irregular dark brown, irregular areas (spots, blotches, speckles, etc.). The ground color of the ventral surface (hyponotum and foot) is creamish after preservation and bears large dark brown blotches that may or may not form a ring around the foot. In addition, there is a fuzzy ring composed by minute brown speckles all around the edge of the hyponotum. Similar speckles are present on the sole and the sides of the foot. Most brown spots and speckles are still present in preserved specimens.

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The width of the foot equals about one third or one half of the width of the dorsal notum (in preserved specimens), except in one specimen in which the foot was narrow (CASIZ 099347). The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are flattened, not grooved, and in most cases clearly ear-shaped (they tend to be less ear-shaped in small specimens). The anterior margin of the oral tentacles of the large specimens is undulated (e.g., ZMUC). Also, the oral tentacles can bear some minute tri-

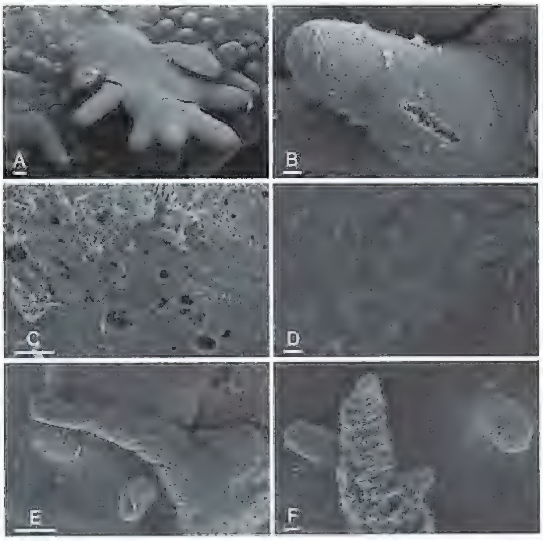

Figure 191. *Asteronotus raripilosa*, dorsal notum. A. Branched papilla, CASIZ 109748 (#1), scale = 100 µm.— B. Tubercle, CASIZ 109748 (#1), scale = 30 µm.— C. Dorsal notum, detail, CASIZ 109748 (#1), scale = 10 µm.— D. Tubercles, CASIZ 070066, scale = 100 µm.— E. Tubercles, CASIZ 070066, scale = 100 µm.— F. Branched papilla, CASIZ 070066, scale = 20 µm.

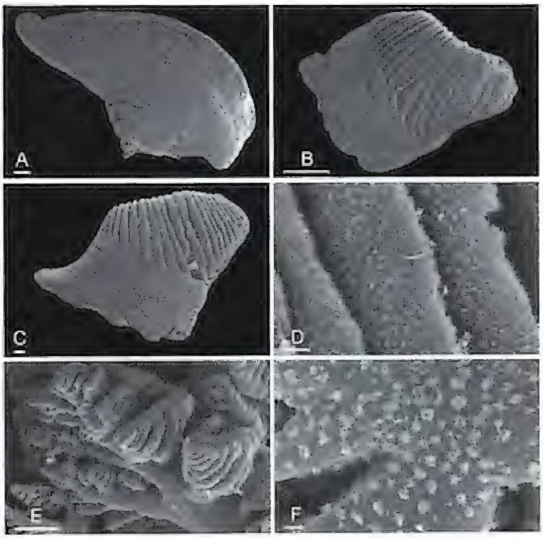

Figure 192. *Asteronotus raripilosa*, oral tentacles, rhinophores, and gills. A. Flattened oral tentacle, CASIZ 109748 (#2), scale = 300 µm.— B. Rhinophore, CASIZ 070066, scale = 1 mm.— C. Rhinophore, CASIZ 109748 (#3), scale = 100 µm.— D. Rhinophoral lamellae, CASIZ 109748 (#3), scale = 30 µm.— E. Branchial plumes, CASIZ 109748 (#3), scale = 200 µm.— F. Branchial plumes, detail, CASIZ 109748 (#3), scale = 20 µm.

angular papillae (not in all specimens though). In addition to non-caryophyllidia tubercles, the dorsal notum bears long, soft papillae, some of which are branched. The number of those papillae (including branched ones) varies a great deal among individuals: one specimen from Japan (CASIZ 070066) has only a few scattered papillae, whereas several other specimens have numerous papillae (e.g., CASIZ 109748, CASIZ 073238). Preservation probably introduces a bias because those papillae are fragile: for example, the type of *raripilosa* bears only a few papillae on the edge of the dorsal notum. The gill opening is distinctly lobate. Many small holes (diameter < 10 µm) and small tufts of cilia were found on the surface of the mantle, including the dorsal tubercles, the papillae, the oral tentacles, and the rhinophores. In preserved specimens, the margins of the rhinophoral and branchial sheaths can be smooth or deeply crenulate. There are six tripinnate branchial plumes arranged in circle around the anus. The rhinophores have from 30 to 45 lamellae.

Digestive system. The stomach is large, free, on top of the left anterior side of the digestive gland. A small caecum is located on the left posterior side of the stomach. The intestine is straight and dorsal. The labial cuticle is armed with a pair of symmetrical jaws. However, the jaws are small compared to the labial cuticle itself, and are not conspicuous. They could easily be overlooked. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. The radular formulae are: 25/30 × (55-0-55) in a 45 mm long specimen (CASIZ 109748, #3); 35 × (75-0-75) in a 65 mm long specimen (CASIZ 109748, #1); 45 × (70-0-70) in a 75 mm long specimen (CASIZ 109748, #2); 45 × (85-0-85) in a 65 mm long specimen (CASIZ 099347); 50 × (90-0-90) in an 80 mm long specimen (CASIZ 070066), 55 × (95-0-95) in an 80 mm long specimen (NMV F16748), 55 × (105-0-105) in an 85 mm long specimen (MCZ 004575), 55 × (130-0-130) in an 100 mm long specimen (ZMUC). The rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, although it tends to peak at about two third of the

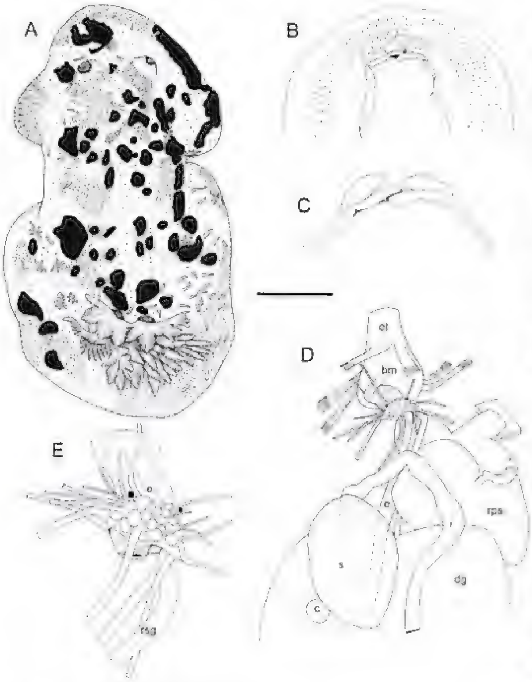

FIGURE 193. *Asteronotus raripilosa*, external morphology and internal anatomy. A. Dorsal view, CASIZ 109748 (#3), total length = 45 mm.— B. Ventral, anterior view, CASIZ 109748 (#1), total width = 40 mm.— C. Oral area (with two oral tentacles), ZMUC, scale = 10 mm.— D. Anterior, internal anatomy, CASIZ 109748 (# 1), scale = 15 mm.— E. Nervous system, CASIZ 109748 (# 1), scale = 2 mm.

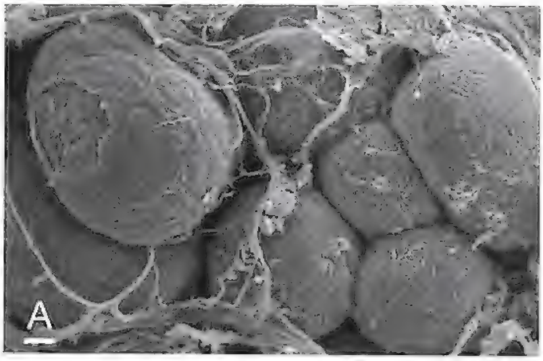

FIGURE 194. *Asteronotus raripilosa*, cerebro-pleural ganglion, dorsal surface, CASIZ 109748 (#3). A. Scale = 30 µm.

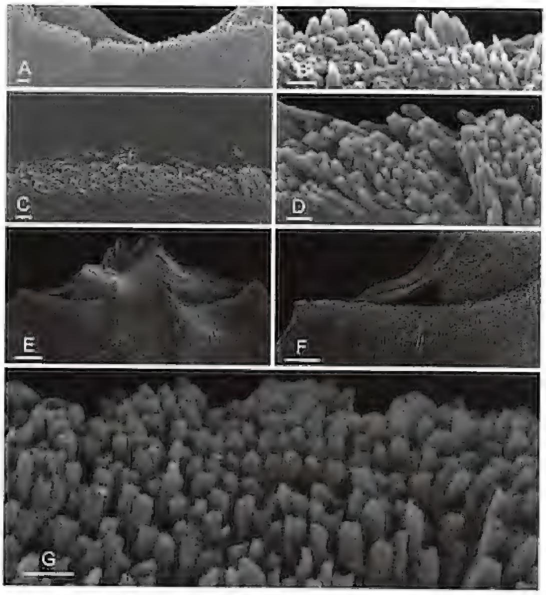

FIGURE 195. *Asteronotus raripilosa*, jaws. A. Jaw rodlets, CASIZ 099347, scale = 30 µm.— B. Jaw rodlets, CASIZ 099347, scale = 10 µm.— C. Jaw rodlets, ZMUC, scale = 20 µm.— D. Jaw rodlets, ZMUC, scale = 10 µm.— E. Two lateral jaws, MV F16748, scale = 200 µm.— F. Jaw rodlets, MV F16748, scale = 100 µm.— G. Jaw rodlets, MV F16748, scale = 10 µm.

row. Also, the size of the four or five innermost teeth size increases gradually, and the size of the last four or five outermost ones decreases gradually. All teeth are hamate, but the last two outermost teeth are often reduced and triangular. The base of the lateral teeth, especially the innermost ones, seems to be much larger than in other species dissected here, although the variation of this feature is difficult to determine. The teeth are not grooved. Except for the four or five innermost and the two or three outermost ones, teeth have outer denticles. The number of denticles increases from one to three and then decreases from three to one, towards the edges. However, some radula have smooth teeth (e.g., MCZ 004575). Also, note that one radula can include both rows with denticulate and rows with smooth teeth. Finally, as rightly pointed by Eliot (1903), the first innermost tooth may not be strictly parallel to the rest of the lateral teeth.

Nervous system. The circum-esophageal nerve ring is relatively short, i.e., its length may equal up to three times the width of the cerebro-pleural ganglia. The cerebral, pleural, and pedal ganglia are fused: large, distinct, spherical masses can be observed on their surface.

Reproductive system. The reproductive system is located on the right side of the body, between

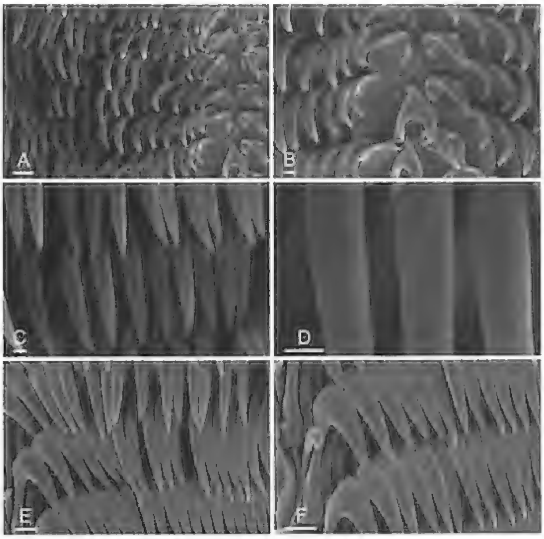

FIGURE 196. *Asteronotus raripilosa*, radula, CASIZ 109748 (#2). A. Innermost teeth, scale = 30 µm.— B. Innermost teeth, scale = 10 µm.— C. Median teeth, scale = 10 µm.— D. Median teeth, scale = 10 µm.— E. Outermost teeth, scale = 30 µm.— F. Outermost teeth, scale = 30 µm.

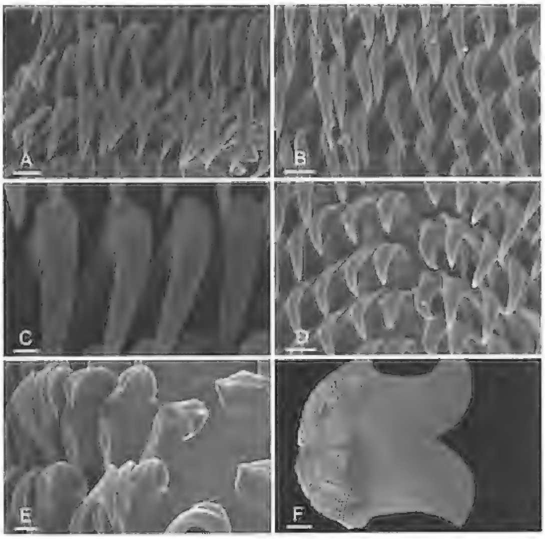

FIGURE 197. *Asteronotus raripilosa*, radula. A.Outermost teeth, CASIZ 109748 (#3), scale = 30 µm.— B. Median teeth, CASIZ 109748 (#3), scale = 30 µm.— C. Median teeth, CASIZ 109748 (#3), scale = 10 µm.— D. Innermost teeth, CASIZ 109748 (#3), scale = 30 µm.— E. Innermost teeth, CASIZ 109748 (#1), scale = 20 µm.— F. CASIZ 070066, scale = 1 mm.

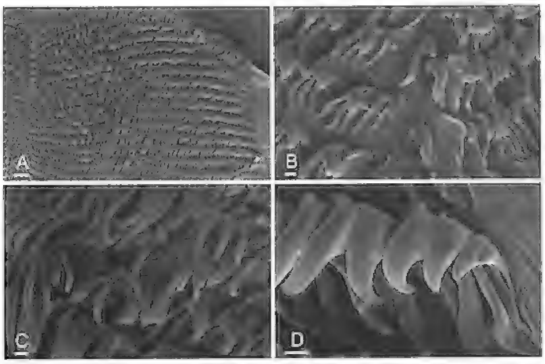

FIGURE 198. *Asteronotus raripilosa*, radula, ZMUC. A. Right rows, scale = 200 µm.— B. Innermost teeth, scale = 20 µm.— C. Median teeth, scale = 30 µm.— D. Outermost teeth, scale = 20 µm.

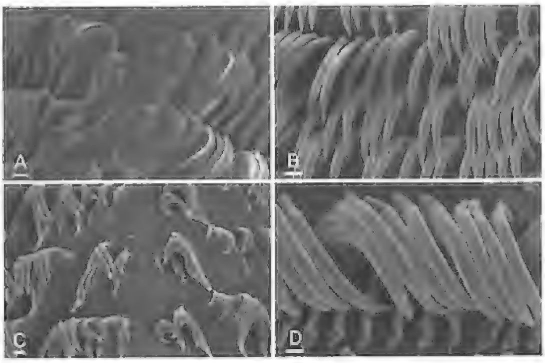

FIGURE 199. *Asteronotus raripilosa*, radula. A. Innermost teeth, CASIZ 099347, scale = 20 µm.— B. Median teeth, CASIZ 099347, scale = 30 µm.— C. Innermost teeth, MCZ 004575, scale = 20 µm.— D. Median teeth, MCZ 004575, scale = 20 µm.

the buccal mass and the digestive gland. The ampulla is tightly convoluted, with up to 20 loops in fully mature animals (but fewer than five in immature animals) before reaching the female gland mass. The division between male and female ducts (in the female gland mass) could not be seen by dissection. The prostate is divided in a proximal whitish part and a distal yellowish part. The deferent duct is straight. A thin tegument, armed with small conical spines covers the inner wall of the distal end of the deferent duct. This inner wall is evaginable, which explains that the distal end of the deferent duct may sometimes looks like a distinct penis covered with small spines (e.g., CASIZ 109748). When the deferent duct is not evaginated, the tegument can be easily separated from the inner wall; the length of the armed tegument can measure up to 20 mm (ZMUC). The

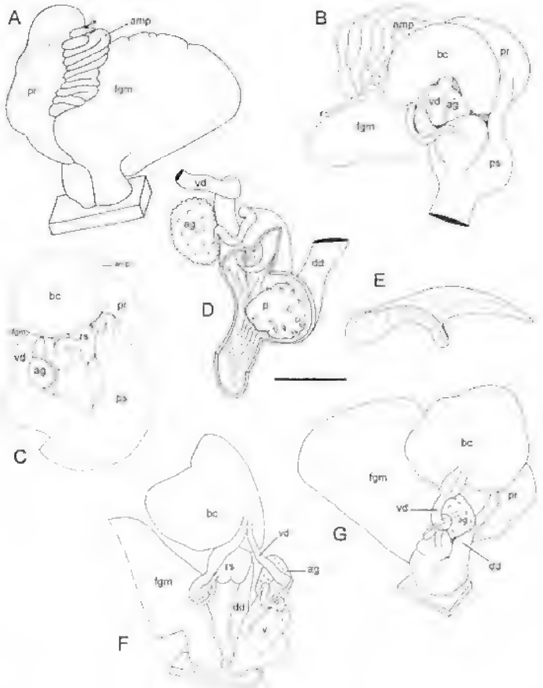

FIGURE 200. *Asteronotus raripilosa*, reproductive system. A. CASIZ 109748 (# 1), scale = 5.5 mm.— B. CASIZ 070066, scale = 6 mm.— C. CASIZ 109748 (#3), scale = 1 mm.— D. Vestibule, vaginal duct and penial sheath opened, CASIZ 109748 (# 1), scale = 2 mm.— E. Hollow spine of the accessory gland, CASIZ 073238, scale = 2 mm.— F. Organs separated, CASIZ 109748 (# 1),scale = 4.5 mm.— G. CASIZ 109748 (# 1), scale = 5 mm.

vaginal duct is loosely convoluted. The deferent duct and the vaginal duct join together and form a vestibule. A distal accessory gland opens into this vestibule. The exact function of this gland is unknown. The gland itself, spherical or ovate, granular, is separated from the vestibule, but communicates with it through a duct. This duct opens into the vestibule through a hollow spine that is conical, curved, with a broad base. It is likely that the product secreted by the gland is released through the hole at the apex of the spine. All specimens had a spine in their accessory vestibular gland, and all spines were deeply curved except in a specimen that, interestingly, had an immature reproductive system (with all structures reduced, in particular the female gland mass, usually well developed in mature specimens). The spine found in this specimen (CASIZ 099347) was conical but straight (note that it was not broken). This suggests that at the beginning of its development, the spine of the vestibular gland is straight and then becomes curved later on. The fertilization duct is loosely convoluted (with one loop). The connection between the fertilization duct and the female gland mass is marked by a clear duct. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is hidden by the receptaculum seminis and the vestibular gland. The bursa copulatrix is about three or four times larger than the receptaculum seminis. The bursa copulatrix, ovate, and the receptaculum seminis, sausage-shaped, are attached to one another.

DIAGNOSTIC FEATURES.— The presence of long, soft, and, more importantly, branched papillae on the dorsal notum is typical of *raripilosa*. This diagnostic character is associated with some other characters such as the ear-like oral tentacles and the lobate branchial sheath, but those characters are present in other species too. A potentially good diagnostic anatomical character is the shape of the curved spine of the accessory vestibular gland, although it can be straight in immature specimens. Other species have a vestibular gland with a hollow spine (e.g., *Asteronotus cespitosus*), but the shape of the spine found in *raripilosa* is unique (at least in mature individuals).

INFRA-SPECIFIC CHARACTER VARIATION.— Anatomical and morphological information available in the literature is largely congruent with observations provided here and improves our understanding of infra-specific variation. Pictures of live animals and descriptions of the color (although usually based on preserved specimens) confirm a broad variation of the dorsal color: e.g., compare the two living animals photographed by Ono (1999).

It seems that there tends to be fewer long, branched papillae in preserved specimens than in live animals, which could be explained by the fact that they are fragile and easily lost or destroyed.

The radular formulae published so far are: 30/40 × (60/70-0-60/70) in a max. 110 mm long

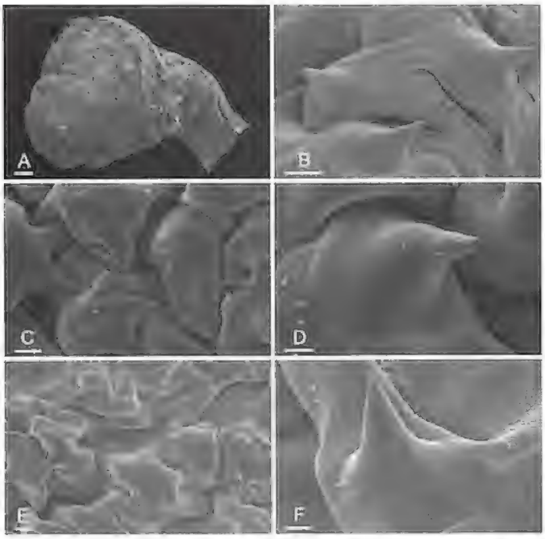

FIGURE 201. *Asteronotus raripilosa*, penial spines. A. CASIZ 109748 (#1), scale = 200 µm.— B. CASIZ 109748 (#1), scale = 100 µm.— C. ZMUC, scale = 200 µm.— D. ZMUC, scale = 100 µm.— E. ZMUC, scale = 200 µm.— F. ZMUC, scale = 100 µm.

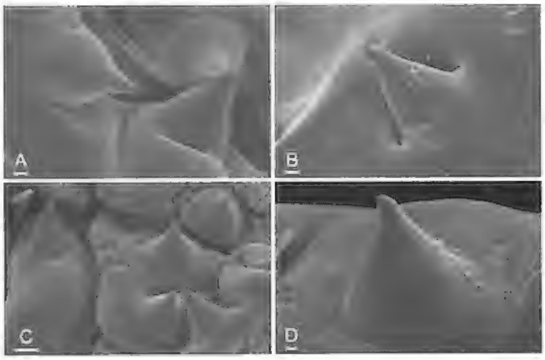

FIGURE 202. *Asteronotus raripilosa*, penial spines. A. MV F16748, scale = 30 µm.— B. MV F16748, scale = 30 µm.— C. CASIZ 070066, scale = 100 µm.— D. CASIZ 070066, scale = 20 µm.

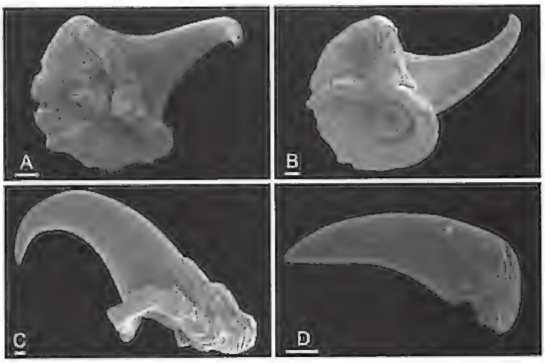

FIGURE 203. *Asteronotus raripilosa*, accessory spines. A. CASIZ 109748 (#1), scale = 200 µm.— B. CASIZ 070066, scale = 200 µm.— C. CASIZ 109748 (#2), scale = 100 µm.— D. CASIZ 109748 (#3), scale = 100 µm.

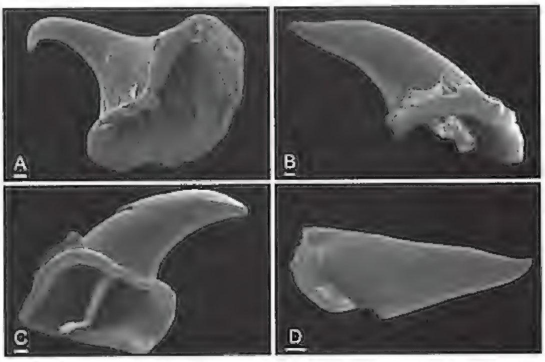

FIGURE 204. *Asteronotus raripilosa*, accessory spines. A. MV F16748, scale = 200 µm.— B. MCZ 004575, scale = 100 µm.— C. ZMUC, scale = 200 µm.— D. CASIZ 099347, scale = 100 µm.

specimen (Eliot 1903, as *papillata*); 33 × (56/58-0-56/58) in a 38 mm long specimen (White 1948, as *winckworthi*); 40 × (80-0-80) in a specimen of unknown size (Eliot 1906b, as *papillata*); 41 × (76-0-76) in a 155 mm long specimen (Valdés 2002, as *Otinodoris* sp.); 48/52 × (91/95-0-91/95) in two 65-68 mm long specimens (Bergh 1880a, as *desmoparypha*); and 50 × (85-0-85) in a 55 mm long specimen (Bergh 1905, as *desmoparypha*). Note that the formula provided by White (1950) was probably an error: 44 × (190-0-190) in an individual of unknown size. Overall, the maximum number of rows is 55 (present study) and the maximum number of teeth per half row is 130 (present study). The radular formulae provided by Narayanan (1968) fit within this range.

Several authors mentioned (and sometimes illustrated) radular denticles: e.g., White (1948, as *winckworthi*) clearly described from three to five outer denticles. The presence/absence of such denticles vary within a single radula and among specimens, which means that no mention of denticles is not surprising (Eliot 1903, 1906b, as *papillata*; Valdés 2002, as *Otinodoris* sp.).

Descriptions of the reproductive system, especially the description of the reproductive system of *desmoparypha* by Bergh (1880a, 1905), fit perfectly with observations provided here. Note that some illustrations of the reproductive system (White 1948, 1950; Valdés 2002) are not considered here because they are not correct (see below).

Discussion.— To say the least, the taxonomy of *raripilosa* is a mess: five specific names (*raripilosa*, *desmoparypha*, *papillata*, *nubilosa*, *winckworthi*) and seven generic names (*Doris*, *Discodoris*, *Hoplodoris*, *Platydoris*, *Sebadoris*, *Otinodoris*) have been used to refer to this species. This confusion mainly results from poor anatomical studies, which prevented authors from realizing that all those names would designate only one species. It also is the result of poor taxonomic practices: the type material of *raripilosa*, informative, seems to have never been examined prior to the present study.

Interestingly, several potential synonymies have been discussed, but never formally proposed. Eliot (1906b, 1910a) suggested a synonymy between *papillata* and *desmoparypha*: "In making an examination of further specimens of this animal, I have found a spine in the accessory gland attached to the female genitalia. The structure of the gland seems to be as described by Bergh for *Hoplodoris*, but the spine is straighter. I cannot help thinking that the species [i.e., *papillata*] is *Hoplodoris desmoparypha*, or at least closely allied to it; but I have not been able to find a labial armature as described by Bergh." (Eliot 1906b:648) Jaws were not found in the specimens dissected here. However, as pointed out in the description, those jaws are not conspicuous. As a matter of fact, jaws were first overlooked in several specimens before it was realized that they actually were present, but small. It is possible that jaws were overlooked by Eliot.

Then White (1950) suggested a synonymy between *desmoparypha* and *raripilosa*, and also mentioned that Eliot considered his *papillata* as certainly equivalent to *desmoparypha*: "This animal [i.e., *desmoparypha*] may be identical with the previously described *Doris raripilosa* Abraham (1877) but until Abraham's specimens are re-examined it is better to retain Bergh's name which is based on an adequate description. It has subsequently been described by Eliot in 1904 as *Platydoris papillata* who later in 1910 stated: « *Pl. papillata* is almost certainly *Hoplodoris desmoparypha* B. »." (White 1950:100) Surprisingly, White did not discuss the fact that the branched papillae she had described in *Otinodoris winckworthi* could be the same as that of *papillata*.

More recently, several authors have discussed the taxonomic status of *Platydoris papillata* Eliot, 1903 and *Hoplodoris desmoparypha* Bergh, 1880, as well as the status of genera such as *Carminodoris* and *Hoplodoris*, but without mentioning most of the earlier literature. Gosliner and Berhens (1998) discussed differences between *Carminodoris* and *Hoplodoris*, and Miller (1991) commented on *Hoplodoris*, but they overlooked the synonymy between *desmoparypha* and other species names, such as *papillata* and *raripilosa*. Dorgan et al. (2002) rightly wrote that *papillata* was not a *Platydoris*, but did not point out, for instance, the possible synonymy of *papillata* with *desmoparypha*, suggested by Eliot (1906b, 1910a).

The treatment of *Hoplodoris desmoparypha* by Fahey and Gosliner (2003) needs to be commented on because it led them to re-allocate species names from *Carminodoris* to *Hoplodoris*. Fahey and Gosliner (2003) asserted that *Hoplodoris desmopharypha* Bergh, 1880 and *Carminodoris mauritiana* Bergh, 1889 —*not* Bergh, 1891, as written in Fahey and Gosliner (2003)— were junior synonyms of *Doris grandiflora* Pease, 1860. Because *desmoparypha* is the type species of *Hoplodoris* and *mauritiana* is the type species of *Carminodoris*, the *ICZN* required Fahey and Gosliner to transfer species names from *Carminodoris* to *Hoplodoris*.

However, the synonymy of *desmopharypha* with *grandiflora* is unlikely, despite the authors' claim: "From our examination, we are certain that our specimens from Palau do in fact represent animals Bergh described in 1880 as *Hoplodoris desmoparypha*. They match almost all features included by Bergh in the original description. There are two primary differences we noted with our specimens. One is that some of the outer lateral teeth have minute denticles on their outer edge that are nearly impossible to see even with a modern compound microscope. We observed them only by high-power scanning electron microscopy (SEM). The second difference is the presence of an armed vagina in our material. This feature could easily have been missed by Bergh." (Fahey and Gosliner 2003:201)

Bergh might have missed the radular denticles (although note that the presence/absence of denticles does vary within a single radula and among individuals). However, it is harder to explain how Bergh could "easily" miss the spines covering the vagina of his specimens given that he published a detailed drawing (Bergh 1880a: plate F, fig. 11) of the open vestibule (where the vagina ends) of *desmoparypha*. More importantly, the spine of the accessory vestibular gland is curved in all Bergh's descriptions of *desmoparypha* (i.e., Bergh 1880a: plate F, figs 11-14; Bergh 1905: plate XV, fig. 2), whereas the spine of the accessory gland described by Fahey and Gosliner is straight. This represents a major difference between the specimens identified by the Fahey and Gosliner as *grandiflora* and Bergh's *desmoparypha*. So far, all anatomical data (including the data published by Fahey and Gosliner) support the hypothesis that *desmoparypha* is not a junior synonym of *grandiflora* or *mauritiana*. Therefore, the species belonging to the same clade as *Carminodoris grandiflora* should be re-allocated to *Carminodoris*. In other words, the species names transferred from *Carminodoris* to *Hoplodoris* by Fahey and Gosliner (2003) should actually be transferred back to *Carminodoris*. Finally, the holotype, by monotypy, of *Carminodoris mauritiana* was actually examined for the present study (ZMB 43939): it now is an empty body wall measuring 25/15 mm, entirely white; it clearly belongs to *Carminodoris* (large papillae on the dorsal notum) and is completely distinct from *Hoplodoris desmoparypha* and *Asteronotus raripilosa*.

The fact that the two most important diagnostic features of *raripilosa* (i.e., branched papillae, a curved, conical, hollow spine of the accessory vestibular gland) have not been described in all original descriptions, needs to be discussed. Especially, it does not weaken the synonymies proposed here. The branchial papillae may be rare in preserved specimens (probably because they are fragile, and also because their number may vary within the species). Because they are rare on the dorsal notum of the type of *raripilosa*, Abraham did not describe them (he simply described the presence of long papillae). Bergh probably did not mention branched papillae *per se* for the same reason, although this may never be verified because the type material is probably lost. A vestibular gland hosting a hollow spine was described in *desmoparypha*, but not in the other species. The present study demonstrated that the absence of description in *raripilosa* was not a real absence (it was found in the holotype). As pointed out above, Eliot (1906b) corrected later his original description of *papillata* when he found a spine in the accessory vestibular gland of new specimens. Finally, the absence of a spine in the original description of *winckworthi* is easily explained by the fact that the reproductive system described by White is largely incomplete and partly erroneous (see remarks on the original description). Note that erroneous descriptions of the reproductive system of *raripilosa* are found even in the recent literature. Re-examination of the specimen CASIZ 073238, recently described by Valdés (2002) as *Otinodoris* sp., showed that Valdés misinterpreted the accessory vestibular gland as the receptaculum seminis, and overlooked both the receptaculum seminis and the hollow spine of the accessory gland in the vestibule. The reproductive system of this specimen measures about 60/40 mm and the hollow spine of the vestibular gland is about 15 mm long.

Several specimens mentioned in the literature are considered to be *raripilosa* because they share some of its characteristics. However, those identities could not be fully verified because no material was available. Marcus and Marcus (1970c) pointed out that the specimen identified by Allan (1947) as *nubilosa* was not *nubilosa* because of the presence of branched papillae on the dorsal notum. The presence of long branched papillae on the dorsal notum of several animals illustrated in field guides (Debelius 1996, as *Sebadoris* sp.; Ono 1999, as *Sebadoris* sp.; Marshall and Willan 1999, as *Otinodoris* sp. 1; Coleman 2001, as *Otinodoris* sp.) indicates that those specimens may be part of *raripilosa*. However, the identification proposed here for the specimen called 'Doridacea sp. 3' by Ono (1999) is more uncertain. White (1948) identified with "difficulty" a 54 mm long preserved specimen from Ceylon as *fragilis*, but the few characters that she provided do not help choose whether she saw *fragilis* or any other species. The presence of "longer papillae, probably branched but too much retracted for details to be made out" and a gill pocket with "six lobes" suggests that White may have seen specimens of *raripilosa*, a species for which she created the new genus and species names *Otinodoris winckworthi* on the same page of the same contribution... Thompson (1975) identified a 120 mm long specimen (alive) from Heron Island, Queensland, as *fragilis*. However, the "broad rather flattened, curved oral tentacles" and the branchial pocket "divided into six valve-like crenulations" of the specimen identified as *fragilis* suggest that Thompson did not observe a specimen of *fragilis*, but rather a specimen of *raripilosa*, although the presence of a "smooth, tapering, and slightly hook-shaped penis" is not compatible with the armed penis of *raripilosa*. Thompson (1975) argued that all previous authors had overlooked the crenulation of the gill pocket as a principal difference between '*concinna*' and '*fragilis*.' Those authors did not overlook this difference: the latter just does not exist! The branchial pocket of *fragilis* is never deeply lobate. Also, the radula formula provided by Thompson, 49 × (117-0-117), is more compatible with *raripilosa* than with *fragilis*. Ortea and co-authors (1981) pointed out that Thompson's identification was problematic, but their comment on Thompson's work was confused by the fact that they also confused *Sebadoris fragilis*, *Tayuva maculosa*, and *Tayuva lilacina*. Anyway, a re-examination of Thompson's material would not change our knowledge of the distribution of *Asteronotus raripilosa*, which is already known from Queensland.

Supra-specific relationships.— The case of *Asteronotus raripilosa* is interesting: it was placed, under different species names, in a total of seven genera. This demonstrates how uninformative taxonomy is if it is not done in a phylogenetic framework. However, some people had some good intuitions... Bergh (1880a) stated that *Hoplodoris (desmoparypha)*, a synonym of *raripilosa*, was intermediary between *Platydoris* and *Asteronotus*: it is true that *raripilosa* shares several characters with *Platydoris* species (5-lobed gill opening, flat tubercles), but those might be due to the large size; it also shares one important feature with *Asteronotus* (the hollow spine of the vestibular gland). Eliot (1903, as *Platydoris papillata*) agreed with him. Other authors expressed different opinions: e.g., Valdés (2002) thought that *Otinodoris* (*Otinodoris winckworthi*, the type species of *Otinodoris*, is a synonym of *raripilosa*) might be a synonym of *Peltodoris*.

A phylogenetic test of the phylogenetic relationships of *raripilosa* shows that *raripilosa* belongs to *Asteronotus*. The Linnaean binomial should be *Asteronotus raripilosa*, which is also a possible name under the *ICPN*. This is quite interesting for the evolution of the dorsal notum. Indeed, *Asteronotus cespitosus*, the type species of *Asteronotus*, is a species with a leathery, smooth, dorsal notum, with no papillae or tubercles. Whereas *raripilosa* is a species with a dorsal notum densely covered with papillae. This suggests that the external morphology should be used with much caution when it comes to determining the supra-specific relationships.

Rostanga Bergh, 1879

Under the *ICZN*, *Rostanga* is a taxon of genus-level. Type-species: *Doris coccinea* Forbes *in* Alder and Hancock, 1848, by monotypy (Bergh 1879a), which is regarded as a synonym of *Rostanga rubra* (Risso, 1818).

The phylogenetic diagnosis of *Rostanga* includes several classes of characters, depending on their phylogenetic significance. 1) One synapomorphy exclusively found in this taxon: lateral teeth slender and elongated (character #19); only this synapomorophy can be regarded as diagnostic of *Rostanga* (i.e., only this character can be used to identify that a species belongs to *Rostanga*). 2) Four synapomorphies of *Discodorididae*: a notched upper lip of the bilabiate anterior foot, digitiform or conical oral tentacles that are *not* expansions of the lateral mouth lips, a flattened prostate divided in two parts of distinct color, and two blood glands. 3) Characters found in many other dorid nudibranchs, e.g., absence of rachidian teeth, labial cuticle armed with jaws —the presence/absence of jaws varies within *Rostanga* according to Rudman and Avern (1989) and Garovoy et al. (2001).

In the present contribution, *Rostanga* refers to a clade name, without being assigned to any particular rank. Under the *ICPN*, *Rostanga* is a converted clade name: it remains an informal clade name until it is phylogenetically defined *and* formally registered. *Rostanga* could be phylogenetically defined through an apomorphy-based definition as "the clade stemming from the first organism or species to possess slender, elongated lateral teeth, as inherited by *Rostanga rubra* (Risso, 1818)."

Rostanga crawfordi **(Burn, 1969) New combination**

Figures 205-208.

Rostanga arbuta.— Burn, 1966:273 [not *arbutus* Angas, 1864].
Discodoris crawfordi Burn, 1969:84-86, figs. 19-24.
Discodoris turia Burn, 1969:86, figs. 25-29. **New synonym.**
Rostanga australis Rudman and Avern, 1989:312-317, figs 1G-H, 2C, 3C, 18C, 19-21, 28. **New synonym.**

Type material (*crawfordi*).— Holotype (NMV F26920), by original designation: one specimen 21/14 mm preserved [30/20 alive], leg. Tom Crawford, 5 March 1963. Two paratypes (WAM S13890, former catalogue numbers WAM 10406 and WAM 10407): two specimens 16/9 (#1) and 13/7 (#2) mm preserved, leg. L. Glauert, June 1923.

Type material (*turia*).— Holotype (NMV F27121), by original designation: one specimen 9/6 mm preserved, leg. Tom Crawford, 24 April 1965.

Type material (*australis*).— Holotype (AM C154817), by original designation: one specimen 32 mm long alive, 6 March 1986. Nineteen paratypes (AM C149545): nineteen specimens from 6 to maximum 32 mm long alive, 6 March 1986. The type material of *australis* was not reexamined. Rudman and Avern mentioned three additional, non-type individuals from South Australia: one 15 mm long specimen, alive, from Eyre Peninsula, and two 5 and 30 mm long specimens, alive, from Yorke Peninsula.

Type locality (*crawfordi*).— Port Phillip, 2 miles NNW of McCrae Lighthouse, near Hovell Pile Light, 15 m depth (dredging), South Channel, Australia. The paratypes were collected from Cottesloe, [Perth], Western Australia.

Type locality (*turia*).— Waratah Bay, Victoria, [Australia].

Type locality (*australis*).— Portsea Pier, 3 meters depth, Port Phillip Bay, Victoria, Australia. All paratypes were collected from the type locality.

Type material condition (*crawfordi*).— The holotype was dissected by Burn. The radula, partly destroyed but still present in the jar, was mounted on a SEM stub for the present study. The labial cuticle and the reproductive system are missing. Burn dissected the paratype #2: the body wall, the digestive gland, and a damaged radula remain. The paratype #1, poorly preserved, was dissected for the present study. Only the radula could be prepared; no structure could be identified in the reproductive system because of the poor condition of the specimen.

Type material condition (*turia*).— The holotype of *turia* was dissected by Burn. Only the body wall remains in the jar. The radula and the reproductive system are missing.

Distribution.— Southern Australia: Victoria (type locality of *crawfordi*, *turia*, and *australis*), South Australia (Rudman and Avern 1989, as *australis*), and Western Australia (paratypes of *crawfordi*). Three records of *crawfordi* have been published in field guides. Two records may be correct: a yellowish, 30 mm long, live animal, identified as *Discodoris crawfordi* by Coleman (1989); a yellowish, 20 mm long live animal, identified as *Discodoris* cf. *crawfordi* by Wells and Bryce (1993:99, fig. 116), from Lion Island, Recherche Archipelago, southern Western Australia. The other record is doubtful: a red, 25 mm long, live animal, identified as *Discodoris crawfordi* by Coleman (2001:55), collected at 15 meters depth, from Bruny Island, Tasmania.

Occurence.— Given the synonymy proposed here, *crawfordi* may not be rare in Victoria where twenty specimens were collected in a single day (holotype and paratypes of *australis*).

WWW.— Two pictures of yellow Japanese dorids identified as *Discodoris* cf. *crawfordi* and *Discodoris crawfordi* have been posted on the *www*. However, these identifications, based only on color similarity, are doubtful. There is no picture of sea slugs identified as *turia* on the *www*. Information about *australis* posted by Bill Rudman on the Sea Slug Forum reproduces Rudman and Avern's (1989) data.

Habitat.— In cavity of a large orange sponge, on sandy bottom (holotype), in a sponge (paratypes). The holotype of *turia* was found "in a large red sponge cast up on the beach." The specimens identified as *australis* by Rudman and Avern were all collected "on colonies of a species of the arenaceous poecilosclerid sponge of the genus *Psammopemma*." Most specimens were collected subtidally.

Literature.— So far, information about the anatomy of *crawfordi*, *turia*, and *australis*, was available only from the three original descriptions. Color pictures of specimens identified as *Discodoris crawfordi* or *Discodoris* cf. *crawfordi* can be found in field guides (Coleman and Willan 1984; Wells and Bryce 1993; Coleman 2001), but the identification of these specimens certainly would need to be confirmed with anatomy. Garovoy and co-authors included *australis* in a phylogenetic analysis of the species of *Rostanga*, but used only some of Rudman and Avern's (1989) data.

Remarks on the original description (*crawfordi*, Figs. 205A, C, 206-208).— Burn described the holotype and the paratypes separately. They also are distinguished here. The color of the living holotype was "apricot-orange with white tips to the papillae and a lighter yellowish notal margin; the sole and hyponotum were bright orange, the branchiae brownish orange, and the rhinophores brown with white apical papilla and white edging to the lamellae at the anterior groove." Burn described the preserved holotype as "grey-orange dorsally and orange ventrally." It currently is homogeneously creamish, colorless. Burn described the color of the paratypes as "dull-yellowish, the larger paratype [i.e., paratype #1] with some reddish-brown areas around the notal margin." Both paratypes currently are dirty creamish-yellowish.

Burn described the notum "wholly covered by closely set 0.2–0.5 mm high cylindrical papillae from the flat top of which 3 to 8 fine brown or hyaline spicules project." These papillae clearly are caryophyllidia, similar to the caryophyllidia found in *Rostanga* and *Jorunna*, i.e., with an elongated peduncle. However, these caryophyllidia are poorly preserved, and the crown of the spicules was hardly recognizable with SEM. A re-examination of the type material confirmed several features: there are no distinct rhinophoral and branchial sheaths in preserved specimens; all specimens have eight branchial plumes (although the exact number is unclear in paratype #1); rhinophores bear about eight oblique (not horizontal) lamellae, with a large apical knob; the oral tentacles are digitiform, but not grooved. The presence of a bilabiate anterior foot with a notched

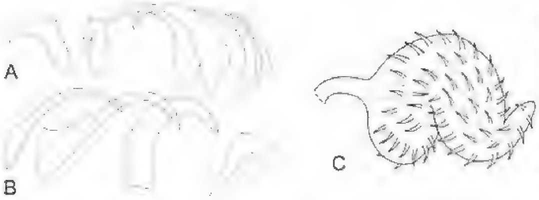

FIGURE 205. *Rostanga crawfordi*, illustrations from original descriptions. A. Radular teeth (number 1, 1, 30, 52, 58, 64), *Discodoris crawfordi*, after Burn (1969: fig. 23).— B. Radular teeth (number 34, 21, 15, 1), *Discodoris turia*, after Burn (1969: fig. 29).— C. Penis, *Discodoris crawfordi*, after Burn (1969: fig. 21).

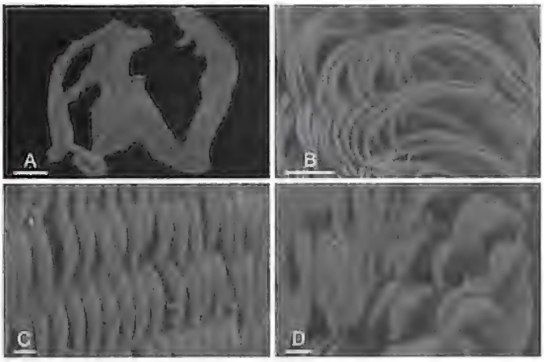

FIGURE 206. *Rostanga crawfordi*, radula, holotype, MV F26920. A. Scale = 600 μm.— B. Outermost teeth, scale = 60 μm.— C. Median teeth, scale = 20 μm.— D. Innermost teeth, scale = 20 μm.

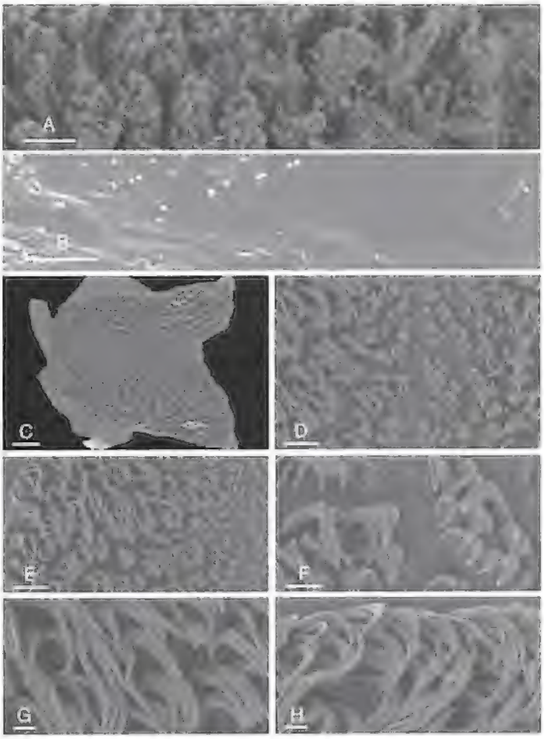

FIGURE 207. *Rostanga crawfordi*, paratype #1, WAM S13890. A. Dorsal notum, caryophyllidia, scale = 40 μm.— B. Smooth labial cuticle, scale = 40 μm.— C. Radula, scale = 400 μm.— D. Innermost teeth, scale = 100 μm.— E. Left rows, scale = 200 μm.— F. Innermost teeth, scale = 40 μm.— G. Median teeth, scale = 40 μm.— F. Outermost teeth, scale = 40 μm.

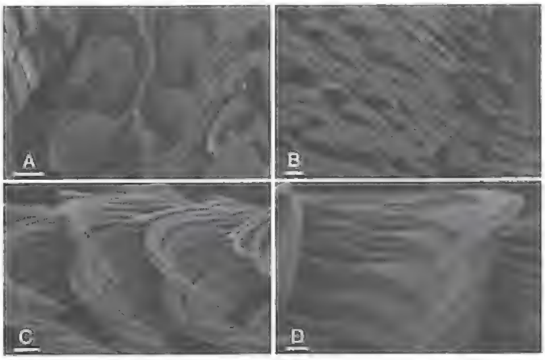

FIGURE 208. *Rostanga crawfordi*, radula, paratype #2, WAM S13890. A. Innermost teeth, scale = 20 μm.— B. Median teeth, scale = 30 μm.— C. Outermost teeth, scale = 20 μm.— D. Outermost teeth, scale = 10 μm.

upper lip, described by Burn, could only be observed in paratype #1 because the oral area of other specimens is largely destroyed.

The labial cuticle is armed with a pair of "small, weak" jaw plates. However, jaw rodlets were not found in paratype #1. The radular formulae given by Burn could hardly be verified because the radulae were largely destroyed. Burn counted 57 × (*c*.54-0-*c*.54) in the holotype, and 50 × (50/60-0-50/60) in paratype #2. However, there may be slightly fewer rows and fewer teeth per row. The radular formula of paratype #1 is 35 × (60-0-60). Burn stated that the rachis was "wide." This could not be verified in the holotype because both sides of the radula were separated. In both paratypes, however, the rachis is not wide. The holotype and the paratypes have similar radulae. The innermost teeth are hamate, with a wide base and a strong hook. The hook of the first innermost tooth bears no denticulation on its inner edge. This also is true in the holotype (Burn described a smooth innermost tooth), but with less certainty: indeed, the radula of the holotype may not be entire and the teeth identified as the first innermost teeth of each row may not be the first ones. The lateral teeth are hamate too, but their hook gradually lengthens towards the edges and gradually becomes narrower, more elongated and more curved. Burn rightly described 10 to 16 marginal teeth as "needle-like," because their base is much shorter than for the rest of the lateral teeth. As Burn pointed out, the transition from innermost to outermost teeth is gradual. The hook of the two outermost teeth may bear an inconspicuous denticle (paratype #2) or bump (holotype and paratype #1). This structure could be seen only with SEM, which explains why Burn did not mention it. Note that this denticulation is not present in all rows within a single radula.

For the reproductive system, Burn described the existence of a "short twice-folded tapering papilla densely armed with minute curved spines" lying "within a distinct flat circular atrium with a narrow aperture" in the paratype #2. Unfortunately, the genital anatomy could not be verified in the holotype and the paratype #2, because it was missing. Also, the reproductive system of the paratype #1 was poorly preserved, and its anatomy could not be re-examined in detail, but it seems that no complex penial structure is present. Finally, Burn mentioned that the holotype had deposited "a beautiful bright pink egg ribbon about 15 cm in length and 5 mm in height. The lower edge was thicker and smooth, the upper edge scalloped and undulate." The shape of the egg ribbon is an important taxonomic feature.

Remarks on the original description (*turia*, Fig. 205B).— The live animal was "cream with sandy speckles." Preserved, it is homogeneously cream, colorless. The cylindrical papillae mentioned by Burn are caryophyllidia with an elongated peduncle. Burn mentioned that they are less dense than in *crawfordi*: this is correct in the median part of the dorsal notum, but not on the edges, where caryophyllidia are dense. The body is narrower in the middle, as pointed out by Burn. Re-examination of type material confirmed several features, such as eight branchial plumes, rhinophores retracted with eight lamellae, a bilabiate anterior foot with a notched upper lip, and conical oral tentacles (not grooved). The radular formula is 39 × (40-0-40): "The simply hamate first lateral is large with a long cusp that lies into the narrow rachis. The succeeding laterals increase in size to about the twentieth tooth, after which the teeth are crowded, longer, very slender and strongly curved. They lie over the inner laterals." Burn created the name *turia* from '*turi*,' an Australian aboriginal word for 'fighting boomerang,' in "allusion to the shape of the marginal radular teeth."

Remarks on the original description (*australis*).— The original description of *australis* is largely complete. It includes information about the variation of several critical characters and notes about the natural history. Here are emphasized the characters that are taxonomically important for species delineation: the color of live animals, the shape of radular teeth, and the egg ribbon. The color varies with the size of the animals and depends on the sponge they feed on as well: "Smaller specimens are translucent white with varying amounts of brown pigmentation forming specks or patches on the dorsal epithelium… One large specimen from South Australia was pale yellow-brown with a microscopic network of white and dark brown specks each colour forming its own irregular reticulate pattern. Around the mantle, just in from the edge, are spherical pale orange-yellow mantle glands. The caryophyllidia are a pale orange-yellow with a set of white specks at the tip between the protruding spicules. A large number of specimens were found in Victoria on an orange sponge. The background colour was a pale orange-pink with a clear submarginal row of opaque mantle glands. In some specimens there was a scattering of brown patches or specks and some white specklings. The caryophyllidia, as in the South Australian specimen, were pigmented." In summary, the color of *australis* varies from "pale yellow-brown to pale orange," acknowledging that "juveniles can be translucent white."

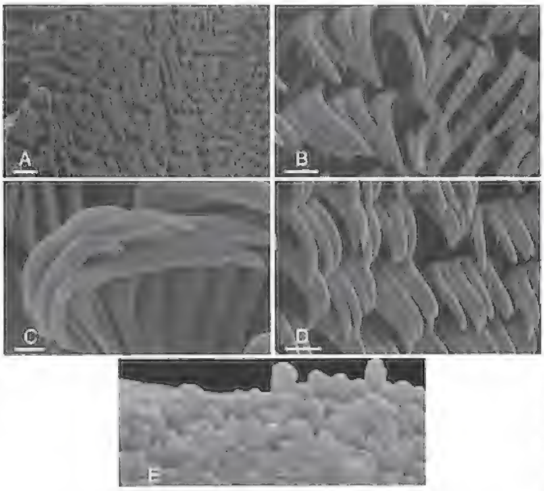

FIGURE 209. Radula and labial cuticle, MV F86411, not *Rostanga crawfordi*. A. Left rows, scale = 100 µm.— B. Innermost teeth, scale = 20 µm.— C. Outermost teeth, scale = 10 µm.— D. Median teeth, scale = 30 µm.— E. Jaw rodlets, scale = 10 µm.

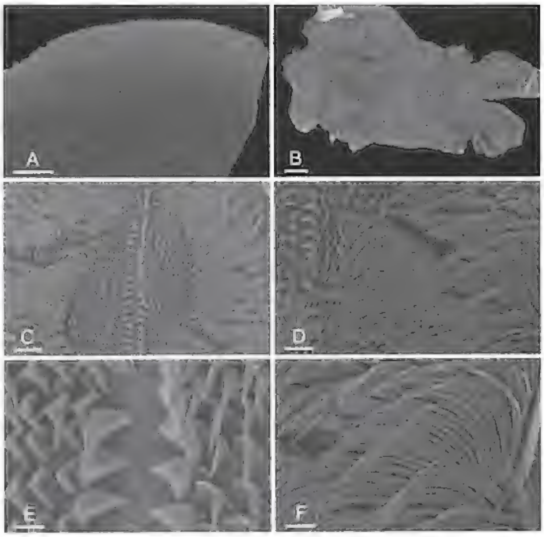

FIGURE 210. MV F86412, not *Rostanga crawfordi*. A. Left jaw plate, scale = 40 µm.— B. Radula, scale = 200 µm.— C. Innermost and median teeth, anterior part of radula, scale = 100 µm.— D. Innermost and median teeth, posterior part of radula, scale = 60 µm.— E. Innermost teeth, scale = 20 µm.— F. Outermost teeth, scale = 40 µm.

Rudman and Avern gave several radular formulae: 36 × 28-0-28 in a 5 mm long specimen, preserved; 40 × (50-0-50) in a 14 mm long specimen, preserved; 41 × (35-0-35) in a 15 mm long specimen, alive; 53 × (50-0-50) in a 17 mm long specimen, preserved; and 56 × (83-0-83) in a 31 mm long specimen, alive. They described the shape of the teeth as follows: "In the largest adult specimen the innermost tooth has a broad base and a recurved hook-like pointed cusp without denticulation. The adjacent lateral teeth are similar in shape and size but gradually lengthen towards the outside. A maximum size is reached about ten teeth from the outside, from where they rapidly reduce in size. The outermost two teeth show some denticulation, with one or two rounded bumps on the outside just below the tip." More interestingly, Rudman and Avern also showed that the degree of denticulation of the innermost tooth and the degree of denticulation of the outermost teeth depend on the size of the animals: in younger specimens, the inside edge of the hook of the first innermost tooth has a fringe of twelve short denticles, whereas this fringe in absent in adult specimens; in younger specimens, up to ten outermost teeth may have up to ten long "bluntly rounded denticles," whereas in adult specimens only the two last outermost teeth have "one or two rounded bumps on the outside just below the tip."

Rudman and Avern did not find any armed penial papilla in the reproductive system of *australis*. However, they described in detail the "pinkish-orange" egg ribbon "arranged in a spiral of approximately three coils. The free edge of the ribbon is densely crenulate." This outer edge of the egg ribbon is also described as "heavily scalloped" by the authors.

DIAGNOSTIC FEATURES.— The diagnostic features are the shape of the radular teeth, acknowledging that it varies among specimens, and the shape of the egg ribbon. The color is problematic because it varies considerably and because several species of *Rostanga* are sympatric in southern Australia (Rudman and Avern 1989).

DISCUSSION.— Several non-type specimens from Victoria identified by Robert Burn identified as *Discodoris crawfordi*, *Discodoris* cf. *crawfordi*, and *Discodoris turia*, were dissected here. However, none of those specimens is part of *crawfordi*. Drawings and SEM pictures of those specimens are available upon request. One 21/15 mm specimen (NMV F30607) from Portsea Jetty, Victoria, identified as *Discodoris* cf. *crawfordi* by Robert Burn, is a caryophyllidia-bearing dorid, but probably not a *Rostanga*; the live animal was white; its reproductive system has accessory ducts that could be *Jorunna*-like accessory glands. Another lot (NMV F86411) from the same locality (Portsea Jetty, Victoria) included three specimens found in an orange sponge and identified as *Discodoris crawfordi*: one 15/11 mm specimen bears caryophyllidia on its dorsal notum, could belong to *Rostanga*, but has radular teeth that differ from that of *crawfordi*, with many denticles, and a labial cuticle armed with jaws (Fig. 209); one 17/11 mm specimen, dissected prior to the present study, is poorly preserved and seems to lack caryophyllidia; one 8/5 mm specimen is poorly preserved and apparently lacks caryophyllidia. One 18/12 mm specimen (NMV F86412) identified as *Discodoris* cf. *crawfordi* by Robert Burn, from Kilcunda Beach, Victoria, belongs to *Rostanga*, but is not part of *crawfordi*, because the shape of the innermost tooth of its radula is incompatible with the variation known in *crawfordi* (Fig. 210). Note that the specimen NMV F30607 or one of the specimens NMV F86411 may be a voucher of a picture of *Discodoris crawfordi* published by Willan and Coleman (1984:37, fig. 110). Finally, four 35/20, 35/20, 30/15, and 20/10 mm specimens (NMV F86443) identified as *Discodoris* cf. *turia* by Robert Burn from Portsea Jetty, Victoria, lack caryophyllidia; these specimens are poorly preserved; it is even unclear whether or not they belong to *Discodorididae*. All those specimens demonstrate that the identification of *crawfordi* is not an easy task, to say the least.

Burn (1966) originally identified the holotype of *crawfordi* as a specimen of *Rostanga arbutus* (Angas, 1864) before Tom Crawford pointed out to him that it might be part of a new species. It is difficult to understand why Burn classified *crawfordi* in *Discodoris* rather than *Rostanga*, because several characters (especially the radula) indicate that *crawfordi* belongs to *Rostanga*. Burn classified *turia* within *Discodoris* too because he thought that it was difficult to distinguish *turia* from *crawfordi*. However, *turia* also present the synapomorphic characteristics of *Rostanga*. Therefore, both *crawfordi* and *turia* must be compared to the species that belong to *Rostanga*. Note that Miller (1996) suggested that *crawfordi* could possibly be part of *Geitodoris* because of its needle-like teeth. This interpretation is incorrect.

Rostanga australis, whose type locality also is from Victoria, shares all the characteristics of *crawfordi*: "*Rostanga australis* is unusual for the genus in not being bright red or orange-red. Specimens have ranged in colour from pale yellow-brown to pale orange, matching the colour of the sponge they are feeding on. Juveniles can be translucent white. The radula is very distinctive with the innermost lateral teeth having a few small inner denticles in juvenile specimens and none in adults. The outermost lateral teeth have four or five short rounded terminal denticles rather than the long rod-like denticles more typical of the genus. The heavily scalloped outer edge to the egg ribbon is also unique" (Rudman and Avern 1989:317).

Two hypotheses can explain this striking similarity between *crawfordi* and *australis*: 1) *crawfordi* and *australis* are synonyms; 2) there are two sympatric, morphologically identical species. The simplest hypothesis must be favored, i.e., *australis* must become a junior synonym of *crawfordi*. This is unfortunate because the original description of *australis* is more complete than the original description of *crawfordi*.

Individual variation, thoroughly addressed by Rudman and Avern (1989) within *australis*, helps us understand that the specimen described as *turia* by Burn probably was a young form of *crawfordi*. Burn (1966:86) admitted that: "In many characters, it is difficult to separate *D. turia* from *D. crawfordi*, both of which occur in sponges. From the latter, *D. turia* differs in the cream not orange body colour, the less dense notal papillation, the slender radula with fewer rows and teeth, and in the slender strongly curved marginal teeth." Infra-specific variation explains easily all these differences. In particular, Rudman and Avern demonstrated that younger specimens were white instead of orange. Burn did not describe any denticulation on the inside edge of the innermost tooth, but he may have overlooked it (his description of the radula is brief and the fine teeth are difficult to see without SEM).

Burn compared *crawfordi* to only two species: *Rostanga arbutus* (Angas, 1864) and *Discodoris dubia* Bergh, 1904. As Burn pointed out, the radulae of *arbutus* and *crawfordi* are very different: in *arbutus*, the inside edge of the hook of the first innermost tooth bears a fringe of strong denticles (Rudman and Avern 1989), whereas the first innermost tooth of *crawfordi* is smooth. This feature does not seem to vary infra-specifically: Rudman and Avern's (1989) work indicates that a species does not include adult specimens with a first innermost tooth both strongly denticulate and smooth. Therefore Burn rightly suggested that *crawfordi* is different from *arbutus*. There is little chance that *Paradoris dubia* and *Rostanga crawfordi* could be confused. Both the external morphology and the internal anatomy are completely distinct (Dayrat 2006). Burn compared those two species because he classified them within *Discodoris* and because they are found in Victoria, but *dubia* belongs to *Paradoris*, and *crawfordi* belongs to *Rostanga*.

The presence of an armed penial papilla in one paratype of *crawfordi* (paratype #2) leads us to an open question: are the specimens from Western Australia part of *crawfordi*? Of course, one cannot exclude that the two paratypes could be part of another species. However, the data currently available do not support this hypothesis. The three types have a similar radula, and no armed penial papilla was found in the paratype #1 (although it was poorly preserved).

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *crawfordi* shows that *crawfordi* belongs to *Rostanga*. The Linnaean binomial for *crawfordi* should be *Rostanga crawfordi*, which also is a possible name under the *ICPN*. *Discodoris turia*, as a junior synonym, is also re-allocated to *Rostanga*.

FUTURE STUDIES.— It would be interesting to address whether or not the *crawfordi* animals from Western Australia produce a diagnostic, heavily scalloped egg ribbon, have an armed penis, and have jaw plates, and also, whether or not *crawfordi* is found in southern Australia, from Victoria to Perth. More broadly, the species diversity of *Rostanga* is poorly known and will require more than just morphological data.

***Rostanga lutescens* (Bergh, 1905)**

Figures 211-213.

Discodoris ? lutescens Bergh, 1905:107-108, plate XIV, figs 22-28 [the epithet is spelled *lutesceus* on page 107, but is changed to *lutescens* on page 248 of the same publication]

Rostanga lutescens.— Johnson and Bertsch, 1985:406-410, figs 1-6.— Rudman and Avern, 1989:329-330.

TYPE MATERIAL.— The holotype, by monotypy, is not held by the Zoological Museum, Amsterdam. It could not be found at the ZMUC, where most of Bergh's collections are. It is probably lost.

TYPE LOCALITY.— Nusa Besi, Timor, Indonesia.

ADDITIONAL MATERIAL DISSECTED.— **Palau**, Ngemelachel Passage, Lighthouse Channel, North Side, from 0 to 16 meters depth, 25 September 1996, one specimen 13/7 mm preserved, leg. T. M. Gosliner, identified as *Rostanga lutescens* by T. M. Gosliner (CASIZ 109725).

ADDITIONAL MATERIAL EXAMINED.— **Papua New Guinea**, north coast, near Madang, Cement Mixer Reef (approximately WNW of Rasch Pass in line with Ruo Island), 21 August 1989, one specimen 7/3 mm specimen, leg. T. M. Gosliner, identified as *Rostanga lutescens* by T. M. Gosliner (CASIZ 068689); **Malaysia**, Sabah, South China Sea, off Kota Kinabalu, Sapi Island, 18 meters depth, 24 July 1991, one specimen 5/4 mm preserved, leg. T. M. Gosliner, identified as *Rostanga lutescens* by T. M. Gosliner (CASIZ 078456); **Philippines**, Luzon Island, Batangas Province, Caban Island, Layag Layag, 21 April 1997, one specimen 8/4 mm preserved, leg. T. M. Gosliner, identified as *Rostanga lutescens* by T. M. Gosliner (CASIZ 110379); **Indonesia**, Sulawesi, Celebes Sea, Manado, Bunaken Island, 1.5 meters depth, 8 May 1990, one specimen 10/5 mm preserved, leg. P. Fiene, identified as *Rostanga lutescens* by P. Fiene (CASIZ 087040); **Hawaii**, Maui, Kapulua Bay, 3 meters depth, 15 May 1997, one specimen 7/3 mm preserved, leg. P. Fiene, identified as *Rostanga lutescens* by P. Fiene (CASIZ 118779).

DISTRIBUTION.— Western Pacific: Timor (type locality), Marshall Islands (Johnson and Bertsch 1985), and possibly Palau (present study). Garovoy and co-authors (2001) have proposed a wide distribution for *Rostanga lutescens* based on some "unpublished material at CASIZ" (from Tanzania up to somewhere in the Pacific – their map is artificially cut on the eastern side). However, this unpublished material was not dissected by those authors. Some CASIZ specimens are mentioned above (one specimen dissected, the rest examined) and indicate potential additional localities for *lutescens*. However, the identity of *lutescens* still is problematic (see below) and all those records should not be taken for granted.

OCCURRENCE.— The occurrence of *lutescens* can hardly be addressed because it still is a poorly known species.

HABITAT.— The three specimens from the Marshall Islands described by Johnson and Bertsch (1985) were collected under dead coral, at five meters depth.

LITERATURE.— Some anatomical data can be found in the original description and in the redescription by Johnson and Bertsch (1985). Rudman and Avern (1989) commented on these publications and Garovoy et al. (2001) introduced *lutescens* in a phylogenetic analysis of *Rostanga* species, but they did not described any new material. A color picture of a live animal was published by Johnson and Bertsch (1985:fig. 1).

REMARKS ON THE ORIGINAL DESCRIPTION.— As Rudman and Avern (1989) pointed out, the original description of *lutescens* is "such that it is very difficult to re-identify this species." Here are only mentioned some of the useful characters that Bergh described. The dorsal notum of the preserved animal (14/7 mm) was yellowish, with dark dots. Bergh had difficulties in determining the anatomy of the radula, although he did notice that there were 25 rows of teeth, the latter being of different shapes depending on their position: the inner tooth bears a small denticle on the external side of its hook; the median teeth are elongate and denticulate; the outermost teeth are simply hamate, with no denticle. This, as pointed out by Johnson and Bertsch (1985:409) is an issue since we would expect to find the elongate, denticulate teeth being the outermost ones (as in other *Rostanga* species). Johnson and Bertsch conclude that Bergh's placement of the teeth was not correct: This statement probably is correct, although we cannot completely exclude that a radula congruent with Bergh's description will be found. Bergh did not write anything informative about the reproductive system.

DESCRIPTION OF A NEW SPECIMEN (CASIZ 109725, Figs. 211-213).— *Color*. The color of the live animal is unknown. Preserved, the specimen is whitish, with a few dark irregular traces of darker blotches.

External morphology. The body is oval. Its length (13 mm) equals almost twice its width (7 mm). The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform and not grooved. The dorsal notum bears long, distinct caryophyllidia. Small holes (diameter less than 10 μm) as well as tufts of cilia are found on the mantle, including the branchial plumes and the rhinophores. In the preserved specimen, the margins of the rhinophoral and branchial sheaths are more or less smooth. There are six tripinnate branchial plumes arranged in circle around the anus. The rhinophores have

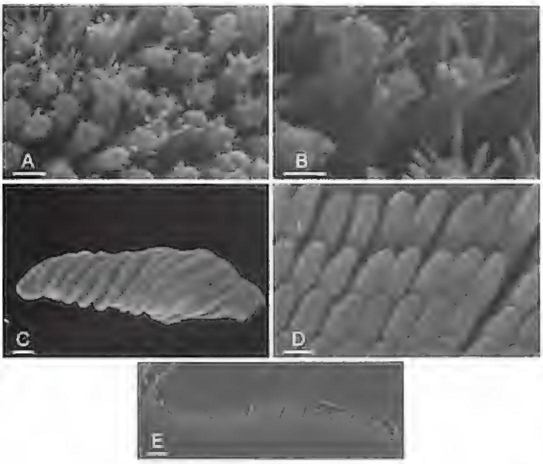

FIGURE 211. *Rostanga lutescens*, CASIZ 109725. A. Dorsal notum, scale = 60 µm.— B. Dorsal notum, scale = 40 µm.— C. Rhinophore, scale = 100 µm.— D. Jaw rodlets, scale = 5 µm.— E. Jaw plate, scale = 30 µm.

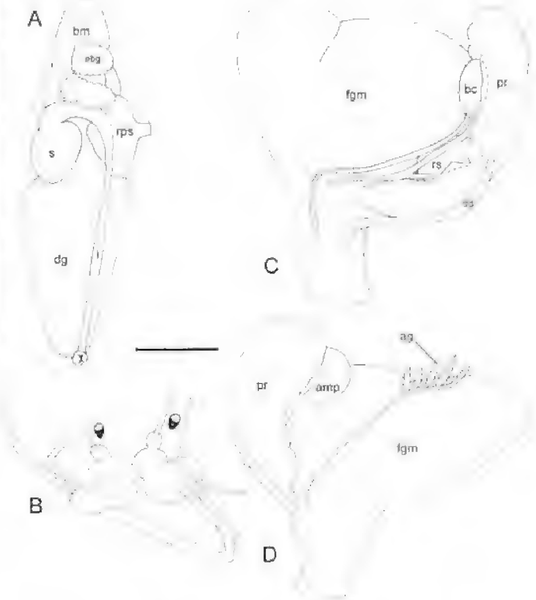

FIGURE 212. *Rostanga lutescens*, CASIZ 109725. A. General anatomy, scale = 2 mm.— B. Nervous system, scale = 0.8 mm.— C. Reproductive system, scale = 0.6 mm.— D. Reproductive system, scale = 0.7 mm.

12 transverse horizontal lamellae.

Digestive system. The stomach is free, narrow, and median. No caecum could be observed by dorsal dissection, although a caecum is present. The intestine is straight and dorsal. The labial cuticle is armed with a pair of jaws. The rodlets are strong, with a head that is consistently rectangular. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. The radular formula is 40 × (18-28-0-28-18) in a 13 mm long specimen. The rachidian teeth are absent. The rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis. Each row is divided in two main zones. The innermost teeth (up to 28) are hamate, with one outer denticle (occasionally two). They are all more or less of the same size, although the first ones may be slightly smaller. The first innermost tooth does not bear inner denticles. Then, in the second, outer zone, the teeth are elongate, with a brush-like tip that consists of long denticles for the innermost ones and shorter denticles for the outermost ones. The transition between the two zones is not gradual.

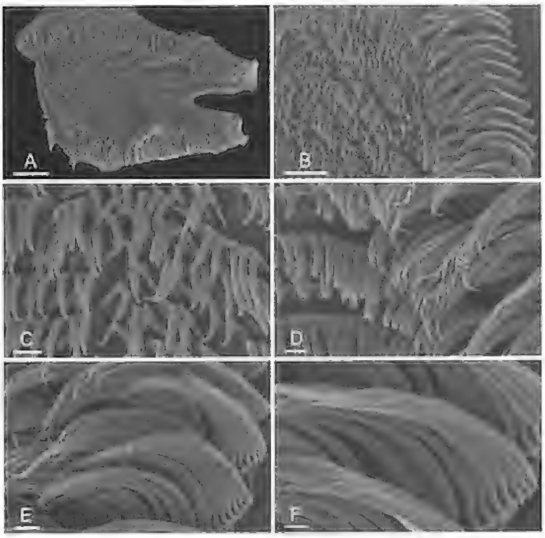

FIGURE 213. *Rostanga lutescens*, radula, CASIZ 109725. A. Scale = 200 µm.— B. Right rows, scale = 100 µm. C. Innermost teeth, scale = 20 µm.— D. Median teeth, scale = 20 µm.— E. Outermost teeth, scale = 20 µm.— F. Outermost teeth, scale = 10 µm.

Nervous system. The circum-esophageal nerve ring is short. Its length equals approximately two or three times the width of the two dorsal cerebro-pleural ganglia. The cerebral and pleural ganglia are fused, although left and right ganglionic centers are separate.

Reproductive system. The ampulla is almost straight (it has just one loop). The division between male and female ducts could not be seen by dissection. The flattened prostate is divided in two parts that are easily recognizable. The deferent duct is straight. No distal accessory gland and no distinct copulatory organ were found. The vaginal duct and the fertilization duct are straight, not convoluted. The connection between the fertilization duct and the female gland mass is marked by a straight, distinct duct. The bursa copulatrix is as large as the receptaculum seminis. The spermatic pouches are ovate and not closely attached to one another.

DIAGNOSTIC FEATURES.— The unclear delineation and infra-specific variation of *lutescens* make it difficult to propose diagnostic features for *lutescens*. The "cream-yellow to light tan" (Johnson and Bertsch 1985:407) color with opaque-white crescents (T. M. Gosliner, pers. com.) seems to be diagnostic, especially because most *Rostanga* species are bright red or orange red. However, the variation of the dorsal color is unknown (the color of *Rostanga crawfordi*, another species that is not bright red, varies from light yellow-brown to light pink-orange, and varies also with the age of the animal; see *crawfordi*). Internal characters also could be useful, especially the shape of the radular teeth. Here again, there is a need to know more about the variation of the denticles before we can propose a diagnostic, radular feature for *lutescens*.

INFRA-SPECIFIC CHARACTER VARIATION.— Let us accept here that Bergh's holotype of *lutescens*, the specimens described by Johnson and Bertsch as *lutescens*, and the specimen dissected in the present study are part of a single unit (but see discussion below). In that case, the innermost tooth may (Johnson and Bertsch 1985) or may not (original description and present study) have some inner denticles, the median teeth may (Johnson and Bertsch 1985; present study) or may not (if the 'outermost' teeth described by Bergh are actually the median teeth) be denticulate. The reproductive system described by Johnson and Bertsch is compatible with the present observations.

DISCUSSION.— At this stage, *lutescens* still is poorly known, and it is unclear that it could be identified easily. We probably can continue to call *lutescens* the light creamy-yellow (with dark blotsches) rostangas that we collect in the tropical Indo-West Pacific, provided that their teeth would be compatible with what has been described so far for *lutescens*. This is what was done here (except that the color of the live animal was unknown).

However, there clearly is a need for a complete taxonomic revision of *Rostanga*, in order to address thoroughly the infra-specific and inter-specific variation. The synthetic work of Rudman and Avern (1989) is great, but several new species have been described in the past few years, and it turns out that several species of *Rostanga* are unusual for their color (i.e., not red or orange) as well as for their radular morphology (e.g., innermost teeth with no inner denticles). Until a complete revision of this group is realized, it cannot be excluded that there are several *lutescens*-like species.

SUPRA-SPECIFIC RELATIONSHIPS.— Clearly, as previous workers have suggested (Johnson and Bertsch 1985; Rudman and Avern 1989; Garovoy et al. 2001), the specimen described as *lutescens* by Bergh belongs to *Rostanga*. It is demonstrated here through a phylogenetic analysis. The Linnaean binomial of *lutescens* should be *Rostanga lutescens*, which also is a possible name under the *ICPN*.

FUTURE STUDIES.— There clearly is a need for a complete taxonomic revision of *Rostanga*, in order to address thoroughly the infra-specific and inter-specific variation. The synthetic work of Rudman and Avern (1989) is outstanding, but several new species have been described in the past few years, and it turns out that several species of *Rostanga* are unusual for their color (i.e., not red or orange) as well as for their radular morphology (e.g., innermost teeth with no inner denticles). An integrative approach using morphological and non-morphological data will be necessary for this revision of *Rostanga*.

***Rostanga rosi* (Ortea, 1979)**
Figures 214-215.

Discodoris rosi Ortea, 1979:575-579, figs 1-4.— Ortea and Urgorri, 1979:75-77, fig. 2.— Urgorri and Besteiro, 1983:22.— Garcia-Gomez, 1983:43.— Rolán and Oterro-Schmitt, 1996:148.— Trainito 2003:36, fig. 91)
Rostanga rosi.— Dayrat and Gosliner, 2005:209-210.

Type material.— Holotype (MNHN, no catalogue number), by original designation: one specimen 5/3 mm preserved, leg. Jesús Ortea, [no collecting date]. Five paratypes were deposited at the department of Zoology of the University of Oviedo, with catalogue numbers P0100-P0105. They were not borrowed for the present study.

Type locality.— Oviñnana (43°30′N, 06°15.4′W), Asturias, Spain.

Type material condition.— The holotype is still entire and globally in good condition, at least externally. It was not dissected for the present study.

Additional material dissected.— [**Mediterranean Sea**, Spain], Málaga, Piedra del Fraile, Fuenqinola, 29 March 1983, one specimen 9/5 mm preserved, [leg. not specified], identified as *Discodoris rosi* by unknown identifier (MNCN 15.05/1972); **Portugal**, Setubal District, Outao, 38°29.36′N, 8°58.48′W, 15 meters depth, 7 May 2002, two specimens 10/6 (#1) and 9/5 (#2) mm preserved, leg. Gonçalo Calado, identified as *Discodoris rosi* by Gonçalo Calado (CASIZ 166874) [the second specimen is poorly preserved, and its internal anatomy is largely uninformative].

Other material examined (not dissected).— Détroit de Gibraltar, Ceuta Nord, Punta Almina, 35°54.1′N, 05°16.5′W, 25-40 meters depth, Mai 1986, one specimen 6/3 mm preserved, leg. [Philippe] Bouchet, [Serge] Gofas, and [Pierre] Lozouet, identified as *Discodoris rosi* by Bouchet et al. (MNHN).

Distribution.— Eastern European Atlantic Ocean and Mediterranean: Asturias and Galicia (Ortea 1979; Ortea and Urgorri 1979; Rolán 1983, cited in Cervera et al. 1988; Urgorri and Besteiro 1983; Rolán and Oterro-Schmitt 1996), Portugal (Dayrat and Gosliner 2005; present study), Atlantic coasts of France (pictures on the *www*), Mediterranean coasts of Spain (Cervera et al. 1988, and references therein; pictures on the *www*), Bahia de Algeciras, Gibraltar (Garcia Gomez 1983), Mediterranean, probably Italy (Trainito 2003).

Gosliner (1987) published a picture of a specimen collected from Algoa Bay, South Africa, with a dorsal color similar to *rosi*. This specimen could not be found and could not be dissected. The presence of *rosi* (or a closely related species) in South Atlantic is thus possible, but not certain.

WWW.— The *www* provides interesting records of *rosi*. In particular, Marina Poddubetskaia collected three specimens from Belle-Ile-en-Mer, Brittany, France, in August 2002: two specimens 20 mm long, alive, at 'La Cathédrale' (11 meters depth), one specimen 15-20 mm long, alive, at 'Penhouet' (Bill Rudman's *Sea Slug Forum* on September 27, 2002, #7812). Belle-Ile-en-Mer is the northernmost locality for *rosi*. Fred Vogt photographed a specimen from Capo de Gata, on the Mediterranean coast of Spain, at 7 meters depth, in August 1993. Luis Sánchez Tocino photographed a specimen 25 mm long, alive, from Punta de San José, Almuñecar, on the Mediterranean coast of Spain, at 8 meters depth, in May 1999. Finally, Michel Barrabés, photographed a specimen 20 mm long, alive, from Hortense, Bassin d'Arcachon, Atlantic coasts of France, on May 08, 1999.

Etymology.— Dedicated to Dr. J. Ros, from the University of Barcelona.

Additional literature.— Cattaneo-Vietti et al. (1990) mentioned the name *Discodoris rosi* as a Mediterranean nudibranch, but did not provide any additional information.

Habitat.— Ortea (1979) found the type specimens in the intertidal zone, under rocks and among algae. Gonçalo Calado collected several specimens by scuba, feeding on the sponge

Clathria (Microciona) gradalis (CASIZ 166874).

Remarks on the original description (Fig. 214).— The dorsal color of live animals was described as orange or red-orange, with with circles, irregularly arranged. The "digitiform papillae" described by Ortea clearly are elongated caryophyllidia. The rhinophores bear from 10 to 15 lamellae. The oral tentacles are digitiform, and not grooved. There are six or seven unipinnate or bipinnate branchial plumes. The labial cuticle is smooth. Ortea described a radula of 100 × (125/145-0-125/145), which seems exceptionally high. However, Ortea acknowledged that he could hardly count the teeth. All teeth are elongated, with a small base and a long hook. The reproductive system includes a vestibular gland, an evaginable penis, a convoluted deferent duct, a flattened prostate, and two spherical spermatic pouches.

Description of new specimens (Fig. 215).— *Color*. The specimens from Portugal were red-orange, with distinct, white circle irregularly arranged on the back (pers. Com. G. Calado). Preserved, the specimens are creamish.

External morphology. The body is oval. Its length equals less than twice its width. The foot is rounded posteriorly and anteriorly. The width of the foot equals about one third or one half of the width of the dorsal notum (in preserved specimens). The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, not grooved. The dorsal notum bears elongated caryophyllidia. Small holes (diameter < 10 μm) and small tufts of cilia could not be found on the surface of the dorsal notum, although they are probably present. There are six or seven bipinnate branchial plumes arranged in circle around the anus. The rhinophores have about 15 lamellae.

Digestive system. The stomach seems to be protected inside the lobes of the digestive gland. The labial cuticle is smooth. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. The number of rows of teeth and the number of teeth per half row could not be determined, but both numbers certainly are less than 100. About 50 rows were counted in one radula (MNCN 15.05/1972), with little confidence though. The teeth are elongated, with a reduced, rectangular base and a long, needle-like hook. The rachidian space is narrow, and there are no rachidian teeth. The size of the lateral teeth is globally constant, although it tends to peak at the two thirds of each row, towards the edge. Also, the innermost and outermost teeth are slightly smaller. The teeth bear no denticles.

Nervous system. The length of the circum-esophageal nerve ring could not be determined with precision. The cerebral and pleural ganglia are fused.

Reproductive system. The reproductive system of the specimens opened was poorly preserved, and probably immature. As a result, nothing could be observed.

Diagnostic features.— The dorsal color (especially the white rings) is diagnostic of *rosi*. Note, however, that, according to Ortea, the ground color varies from light yellow to almost black (Bill Rudman's *Sea Slug Forum*, September 27, 2002, #7812). However, most specimens found are orange. The specimens identified as *rosi* by Trainito (2003) were bright red.

Discussion.— So far, this species has not been confused with any other species. However, it is still poorly known. Its reproductive system (e.g., the penial structure, the vestibular gland) needs to be described more thoroughly. The infra-specific variation of most anatomical features is unknown.

Supra-specific relationships.— Dayrat and Gosliner (2005) re-allocated *rosi* to *Rostanga*, based on a phylogenetic analysis. This result is confirmed here.

Future studies.— Infra-specific variation of anatomical features will need to be addressed in combination with the dorsal color. In addition, it would be interesting to determine whether or not the animals found in South Africa with a *rosi*-like dorsal color (Gosliner 1987) are part of *rosi*

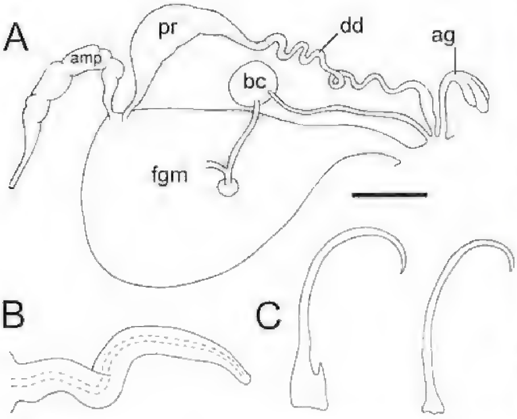

FIGURE 214. *Rostanga rosi*, after Ortea (1979: figs 3-4). A. Reproductive system, scale = 200 µm.— B. Penis.— C. Radular teeth, scale = 30 µm.

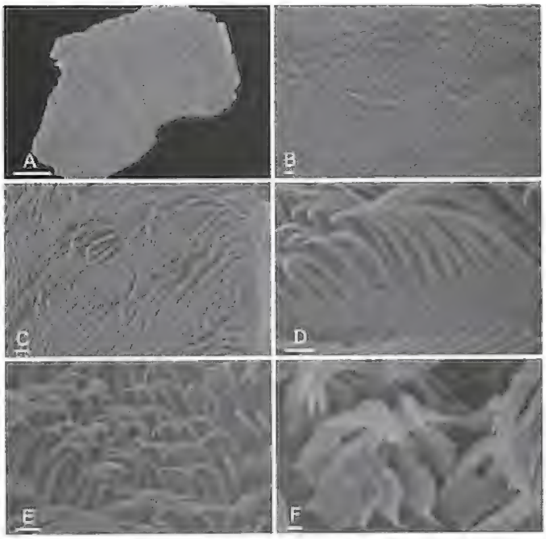

FIGURE 215. *Rostanga rosi*, radula. A. MNCN 15.05/1972, scale = 200 µm.— B. Innermost and median teeth, MNCN 15.05/1972, scale = 20 µm.— C. Outermost teeth, MNCN 15.05/1972, scale = 20 µm.— D. Median teeth, detail of tooth foot, MNCN 15.05/1972, scale = 10 µm.— E. Innermost teeth, MNCN 15.05/1972, scale = 10 µm.— F. Innermost teeth, CASIZ 166874, scale = 3 µm.

or a distinct entity. Generally speaking, as always, it would be great to determine whether *rosi* is a highly polymorphic species or one species complex with cryptic species.

Paradoris Bergh, 1884

Under the ICZN, *Paradoris* is a taxon of genus level. Type species: *Paradoris granulata* Bergh, 1884, by monotypy, which is regarded as a synonym of *Paradoris indecora* (Bergh, 1881). For the diagnosis and revision of *Paradoris*, see Dayrat (2006). In the present contribution, however, *Paradoris* refers to a clade name, without being assigned to any particular rank. A few comments on the *Paradoris* species originally classified in *Discodoris* are added here.

Paradoris cavernae (Starmühlner, 1955)

Discodoris cavernae Starmühlner, 1955:219-223, figs 5-9.

DISCUSSION.— *Discodoris cavernae* is one of the four synonyms recently proposed for *Paradoris indecora*, a species known from the Mediterranean and the eastern Atlantic Ocean. The type locality of *cavernae* is near Naples, Italy (Dayrat 2006). A reference was previously overlooked: Starmühlner (1968) mentions that *Discodoris cavernae* is often associated with *Peltodoris atromaculata* in caves.

Paradoris dubia (Bergh, 1904)

Discodoris dubia Bergh, 1904:50-51, plate III, figs 29-30, plate IV, figs 1-2.
Paradoris dubia.— Dayrat & Gosliner, 2005:204, 209-213, 222.— Dayrat, 2006:135, 140-155, figs 5-16.

DISCUSSION.— *Paradoris dubia* is the valid name for a species recorded from New Zealand, New South Wales, Victoria, Tasmania, South Australia, and Western Australia. Its type locality is on the north-western coast of Tasmania. Its anatomy was recently described and its taxonomy revised (Dayrat 2006). The latter publication is available for more information. *Paradoris dubia* can be identified with its genital anatomy (note that it also is the only species of *Paradoris* known from those waters). There are three synonyms for *Paradoris dubia*: *Discodoris egena* Bergh, 1904, and *Alloiodoris nivosus* Burn, 1958, recognized as synonyms by Burn (1969), as well as *Paradoris leuca* Miller, 1995, recognized as a synonym by Dayrat (2006). An additional reference, previously overlooked, is added here: Burn (1989:766, figs 12.12, plate 52, fig. 2) briefly mentioned *dubia* in a field guide on the marine invertebrates of southern Australia; he presented it as a common, widely distributed species, from Cape Naturaliste, Western Australia, up to Tasmania and Victoria, and found up to 40 meters depth. Burn's (1989) brief description does not add anything to our knowledge of the character variation, especially given that internal anatomy is not discussed.

Paradoris egena (Bergh, 1904)

Discodoris ? *egena* Bergh, 1904:54-55, plate III, fig. 31, plate IV, figs 7-14.

Discussion.— This name was recognized as a synonym of *Discodoris dubia* Bergh, 1904, by Burn (1969), before Dayrat and Gosliner (2005) transferred *dubia*, and thus *egena* too, to *Paradoris*. The type locality of *egena* is the same as the type locality of *dubia*, i.e., north-western coast of Tasmania. The anatomy of *Paradoris dubia* was recently described and its taxonomy revised (Dayrat 2006). The latter publication is available for more information.

Paradoris erythraeensis (Vayssière, 1912)

Discodoris erythraeensis Vayssière, 1912:23-24, figs 150-152.
Paradoris erythraeensis.— Dayrat, 2006:135, 155-171, figs 17A-C, 18-33.

Discussion.— *Paradoris erythraeensis* is a valid name for a species recorded from Djibouti, Suez Canal, Red Sea, Tanzania, South Africa, Thailand, Indonesia, and the Philippines. Its type locality is in Djibouti. Its identification is difficult, and it may include more than one unit. More information on its anatomy and revised taxonomy can be found in Dayrat (2006). Recently, Camacho-García and Gosliner (2007) proposed that *erythraeensis* included more than one species, and described a new species from South Africa: *Paradoris caeruleus*. Yonow (2008) published two pictures of *erythraeensis* from the Red Sea.

Paradoris indecora (Bergh, 1881)

Discodoris indecora Bergh, 1881:108-112, plate J, figs 26-33, plate K, figs 11-19.
Paradoris indecora.— Templado, 1984:519.— Dayrat, 2006:135, 171-188, figs 34-44.

Discussion.— *Paradoris indecora* is the valid name for a species recorded from the Mediterranean and eastern Atlantic Ocean (Portugal, Morocco, and the Canary Islands). Its type locality is Trieste, Italy. Its anatomy was redescribed recently and its taxonomy revised (Dayrat 2006). No diagnostic feature for *indecora*, but it is the only *Paradoris* species known from the Mediterranean and the eastern Atlantic Ocean. Its dorsal color could be diagnostic but its infra-specific variation is poorly known. There are five synonyms for *Paradoris indecora*: *Paradoris granulata* Bergh, 1884, the type species of the genus *Paradoris*, recognized as a synonym by Ortea (1995), as well as *Paradoris ceneris* Ortea, 1995, *Paradoris inversa* Ortea, 1995, *Paradoris mollis* Ortea, 1995, and *Discodoris cavernae* Starmühlner, 1955, all recognized as synonyms by Dayrat (2006). The latter publication is available for more information.

A few references previously overlooked are added here, although those references do not change anything to our knowledge of the distribution or anatomy of *indecora*: Nordsieck (1972:61, fig. 11) briefly mentioned the presence of *Paradoris granulata* from the Mediterranean; Schmekel (1968:115) mentioned (with no description) specimens of *indecora* from the Gulf of Naples; Perrone (1986:36) mentioned one specimen of *Discodoris indecora* from the Gulf of Taranto, Mediterranean; Riedl (1983:337, plate 117) published a imprecise black-and-white drawing. Trainito (2003:34, figs 82-83) published two pictures of two color variants of *Paradoris indecora* (Mediterranean localities are not specified). Finally, Pruvot-Fol (1951) thought that Delle Chiaje's (1822) *Doris testudinaria* could be a synonym of *Discodoris indecora* Bergh, 1881, but it is nearly impossible to understand what Delle Chiaje or even Risso (who first named *Doris testudinaria*) actually saw (see *Doridina testudinaria* for discussion).

Finally, the name *Doris porri* Verany, 1846, regarded as a possible synonym of *indecora* by Ortea (1995), is commented on. Ortea rightly pointed out that Verany (1846:97) did use the name "*Doris Porri*," in addition to "*Doride di Porro*." The name *Doris Porri*, accompanied by a description (Verany 1846:102), is valid. However, it is difficult to guess what Verany was referring to from the original description because the latter did not include any drawing. However, a manuscript written by Verany in the 1850s was recently published (Verany 2001). The color illustration that Verany drew for *Doris Porri* clearly suggests that *Doris Porri* refers to the same species as *indecora*. Verany's name, a senior synonym, should have priority. However, *Doris porri* has not been used as a valid name since 1899: Pruvot-Fol (1954a:289) wrote that *Doris porri* was a *Discodoris*, but mentioned it as an *incertae sedis*. Also, *indecora* was cited in 26 works since 1956, either as *Discodoris indecora* or *Paradoris indecora* including the references added here (Dayrat 2006). In such circumstances, the ICZN Article 23.9 applies because both 23.9.1.1 and 23.9.1.2 are met. Therefore, starting from the date of publication of this monograph, *Paradoris indecora* will have precedence over *Doris porri*.

Paradoris liturata (Bergh, 1905)

Discodoris ? liturata Bergh, 1905:106-107, plate XIV, figs 15-20.
Paradoris liturata.— Dayrat & Gosliner, 2005:209, 223, figs 4F, 5A-B.— Dayrat, 2006:135, 188-195, figs 17D-H, 45-51.
Aldisa sp. 2 Yonow, 2008:156, two unnumbered figures.

Discussion.— *Paradoris liturata* is the valid name for a species recorded from Indonesia and Papua New Guinea. Its type locality is in Indonesia. It can be identified with its peculiar, *Phylidiella*-like, dorsal color. Its anatomy was recently described and taxonomy revised (Dayrat 2006). Tonozuka's (2003:109, fig. 141) *Discodoris* sp. B, from Rinca Island, Indonesia, 12 meters depth, is part of *Paradoris liturata*. Also, the two specimens identified as *Aldisa* sp. 2 by Yonow (2008) very likely are part of *Paradoris liturata*, which is very interesting because it significantly increases its distribution and suggests that *liturata* might be present (although likely rare) in the entire Indian Ocean.

Paradoris lora (Marcus, 1965)

Discodoris lora Marcus, 1965:273-274, figs 14-18.
Paradoris lora.— Dayrat, 2006:135, 197-199, fig. 53.

Discussion.— *Paradoris lora* is known from a single specimen collected from the Caroline Islands (Dayrat 2006). *Paradoris lora* is a *nomen dubium*.

Geitodoris Bergh, 1892

Under the *ICZN*, *Geitodoris* is a taxon of genus-level. Type-species: *Doris complanata* Verrill, 1880, by monotypy.

The phylogenetic diagnosis of *Geitodoris* includes five classes of characters, depending on their phylogenetic significance. 1) One synapomorphy exclusively found in this taxon: pectinate outermost teeth, five to ten of which are fused together; only this synapomorphy can be regarded as diagnostic of *Geitodoris* (i.e., only this character can be used to identify that a species belongs to *Geitodoris*). 2) Four synapomorphies of *Discodorididae*: a notched upper lip of the bilabiate anterior foot, digitiform or conical oral tentacles that are *not* expansions of the lateral mouth lips, a flattened prostate divided in two parts of distinct color, and two blood glands. 3) Characters found in many other dorid nudibranchs, e.g., absence of rachidian teeth, hamate lateral teeth, etc. 4) A character also found in *Paradoris*: wide hole in the dorsal notum, which are openings of mantle glands that produce an acidic secretion (this feature may be a synapomorphy for a clade including *Geitodoris* and *Paradoris*). 5) Characters that are found in other discodorids although their exact phylogenetic significance is still unknown, e.g., the presence of a distal accessory gland.

In the present contribution, *Geitodoris* refers to a clade name, without being assigned to any particular rank. Under the *ICPN*, *Geitodoris* is a converted clade name: it remains an informal clade name until it is phylogenetically defined *and* formally registered. *Geitodoris* could be phylogenetically defined through an apomorphy-based definition as "the clade stemming from the first organism or species to possess pectinate outermost teeth, as inherited by *Geitodoris complanata* (Verrill, 1880)."

Geitodoris species are not described in detail because a revision of that clade will be published separately. A few issues related to the use of the name *Discodoris* are discussed.

Geitodoris fulva (O'Donoghue, 1924) New combination

Discodoris fulva O'Donoghue, 1924b:27-28.

Type material.— The description of *fulva* was based on a single specimen that was not designated as the type. O'Donoghue did not mention where this specimen was deposited. It is neither at the Museum of British Columbia nor at the Natural history Museum, London. O'Donoghue was a professor at the University of Manitoba, but this university does not seem to hold any of his collections. This holotype, by monotypy, was probably never deposited, and is probably lost. Given its length (5.25 mm), it likely was destroyed for the description.

Type locality.— Biological Station at Nanaimo, Vancouver Island, British Columbia, northeastern Pacific.

Distribution.— The holotype is the only specimen known.

Discussion.— Ernst Marcus (1961) rightly proposed that *fulva* was a young specimen of *Discodoris heathi* (see below). The taxonomy of *fulva* will be addressed separately in a revision of *Geitodoris*.

Geitodoris heathi (MacFarland, 1905)

Discodoris heathi MacFarland, 1905:39-40.
Geitodoris heathi.— Behrens, 1991:68, unnumbered figure.

Type material.— Holotype (NMNH 181282), by original designation: one specimen 25/15 mm preserved, leg. F. M. MacFarland, June 1897. The Natural History Museum, London, holds two topotypes (NHM 1953.6.30.341-342) from Point Pinos, California: two specimens 11/9 and

10/8 mm preserved, leg. C. H. O'Donoghue, [no collecting date]. However, topotypes are not part of the type material.

Type locality.— Pacific Grove, Monterey Bay, California.

Type material condition.— The holotype is still entire and externally well preserved, which suggests that MacFarland used more than one specimen to describe *heathi*, although just a single type was deposited. The two topotypes from the NHM are in poor condition (they probably dried for a while).

Distribution.— Eastern Pacific, from Alaska to Baja California (e.g., Behrens and Hermosillo, 2005).

Discussion.— The anatomy and the taxonomy of *heathi* will be published separately, in a revision of *Geitodoris*.

Geitodoris mavis (Marcus and Marcus, 1967)

Discodoris mavis Marcus and Marcus, 1967a:187-189, fig. 46.
Geitodoris mavis.— Shrödl, 2000:208.

Type material.— Holotype (NMNH 678407), by monotypy: one specimen 15/9 mm preserved, leg. P. Pickens, 5 March 1966. The label does not specify whether or not this specimen of *Discodoris mavis* is a type. However, it likely is the holotype because: 1) the information on the label (collecting date, locality, etc.) corresponds exactly to the information published by the Marcus in the original description of *mavis*; 2) the label also refers to the Marcus' (1967) contribution where *mavis* was described; 3) the original description was based on a single specimen.

Type locality.— Puerto Peñasco, Sonora, Mexico, [northeastern Gulf of California].

Type material condition.— The holotype was entirely dissected by Eveline and Ernst Marcus. All the internal organs are missing, except for the digestive gland. The labial cuticle and the radula are preserved on a slide (F-912) in poor condition (it is completely dry). No slide was found for the reproductive system. A piece of dorsal notum was cut prior to the present study.

Distribution.— Gulf of California.

Discussion.— The anatomy, the taxonomy, and the distribution of *mavis* will be addressed separately, in a revision of *Geitodoris*. As suggested by Shrödl (2000), *mavis* belongs to *Geitodoris*.

Geitodoris planata (Alder and Hancock, 1846)

Doris planata Alder and Hancock, 1846:292-293.— Alder and Hancock, 1847: fam. 1, plate 8, figs 1-7.— Alder and Hancock, 1855:42.
Doris testudinaria.— Alder and Hancock, 1862:261-262.— Alder, 1969:85 [may or may not be *Doris testudinaria* Risso, 1818].
Platydoris ? planata.— Bergh, 1878a: XXXIII.
Platydoris planata.— Garstang, 1889:178.
Geitodoris planata.— Eliot, 1904:180-181.
Discodoris planata.— Bouchet and Tardy, 1976:212 [with a wrong date for the authorship "Alder and Hancock, 1845"].— Thompson and Brown, 1976:132-133, figs. 69.

Type material.— The holotype, by monotypy, could not be found and is probably lost. However, a slide with a radula and a labial cuticle was found at the Hancock Museum which are part of the holotype. The Hancock Museum holds two specimens and three slides from Alder and Hancock's material labeled as *planata* or *testudinaria*. The labels, of course, are of primary importance. Contrary to what Eliot (1906d) and Valdés (2002) have asserted, the slides and specimens labeled as *testudinaria* are not part of the type material. They may be part of specimens of *planata*, but that is a completely separate issue. The original description of *planata* was based on a single specimen collected from Lamlash Bay, Isle of Arran, off the western coast of Scotland. Therefore, only the material labeled as *planata* and collected from the type locality can be part of the holotype, by monotypy. There is no other possible type material. Alder and Hancock used the species name *Doris planata* for only one specimen: the holotype of *Doris planata*. They referred to that specimen from Lamlash Bay three times, in 1846, 1847, and 1855. Subsequently, they never referred to any new specimen as '*Doris planata*.' The Hancock Museum does not hold any specimen labeled as '*planata*,' and the holotype is probably lost. However, there is a slide (NEWHM 3/23/36) with a label on which is written: "*D. planata*, Scotland" and "*D. planata nec D. testudinaria*, Scotland [..?..] Alder, 1863." This slide is part of the holotype of *Doris planata*.

This label clearly indicates that, in 1863, Eliot wanted to point out that *planata* was not the same as *testudinaria*. In fact, we know that Alder and Hancock (1862) regarded *testudinaria* and *planata* as two distinct species. We also know that Alder and Hancock (1862) knew only two specimens, one of each species: one specimen collected from Herm Island by R. S. Brady and G. Hodge was referred to as *Doris testudinaria*; and the holotype of *planata*, from the Isle of Arran, was still referred to as *Doris planata*.

The specimen from Herm Island is at the Hancock Museum (NEWHM: 2002.H2573). Its current label says: "Type specimen, radula extracted probably by A. + H., *Doris testudinaria* Herm." This label, which is not the original label, probably was written during Eliot's period. Indeed, Eliot (1906d:341) wrote: "Alder and Hancock's type specimen labeled "*Doris testudinaria* Herm," has been kindly sent to me by the Council of the Hancock Museum, Newcastle." It seems that someone from the Hancock Museum sent this specimen to Eliot as a type, although it is also possible that Eliot thought that it was a type and that the label was made based on his work. In any case, one thing is clear: it is not a type. It is obviously not the type of *Doris testudinaria* Risso. It is not the type of *Doris planata* either because: 1) the label refers to it as *testudinaria* instead of *planata*; and 2) it was collected from Herm Island, one of the Channel Islands, near Guernsey, which is quite far from the Isle of Arran, the type locality. Note that Alder and Hancock knew only one specimen of *testudinaria* from Herm Island. Therefore, the specimen held by the Hancock Museum (NEWHM: 2002.H2573) and labeled as "Type specimen, radula extracted probably by A. + H., *Doris testudinaria* Herm" is not a type specimen, but is the specimen that Alder and Hancock (1862) referred to as *Doris testudinaria* and that they thought was distinct from *Doris planata*. Note that the Hancock Museum also holds two slides (NEWHM 3/23/41 and 3/23/46) labeled as "*Doris testudinaria*," each with a radula and a labial cuticle. One of those slides should be part of the specimen from Herm.

Alder (1869) changed his mind about *planata* and *testudinaria*: he regarded them as synonyms, with the holotype of *planata* from Arran Island being a young *testudinaria*. In 1869, Alder added a third specimen to the two previously known ones: one specimen collected near Cumbrae (i.e., Cumbray), Firth of Clyde, off western coast of Scotland. Because Alder (1869) accepted *Doris testudinaria* as the valid name, he logically referred to that specimen from Cumbrae as *Doris testudinaria*. This specimen is held by the Hancock Museum (with no catalogue number). It is simply labeled as "*Doris Testudinaria*, Cumbray Island." Valdés (2002) thought that this specimen was a syntype of *Doris planata*. It cannot be a syntype of *Doris planata* for three reasons. First, *Doris planata* was described based on a single specimen, and therefore the type material consists of a holotype by monotypy, not syntypes. Second, this specimen was not collected from the type locality: the Small Cumbray and the Great Cumbray islands are close to Arran Island (which is also in the Firth of Clyde), but they are not the same islands. Third, it is identified as *Doris testudinaria*, not *Doris planata*, which is quite problematic for a name-bearer of *Doris planata*. Finally, the Hancock Museum also holds two slides (NEWHM 3/23/41 and 3/23/46) labeled as "*Doris testudinaria*," each with a radula and a labial cuticle. One of those should be part of the specimen collected from Cumbray by Robertson.

Between 1846 and 1869, Alder and Hancock (1846, 1847, 1855, 1862) and Alder (1869) mentioned three specimens of *Doris testudinaria*, one of them being the holotype of *Doris planata*, which Alder (1869) then regarded as a young of *Doris testudinaria*, and two specimens that they identified directly as *Doris testudinaria*. The fact that those specimens were collected from three different localities (Arran Island, Herm Island, and Cumbray) makes it possible to identify them with precision in the Hancock Museum collection, which holds only three specimens (two specimens and three slides). Note that, Alder (1869:85) mentioned a few records for *Doris testudinaria* in addition to Arran Island, Herm Island, and Cumbray: three from the Mediterranean (Nice, Adriatic Sea, Aegean Sea) and Falmouth. However, it is unclear whether or not Alder and Hancock had specimens from those localities. More importantly, those records do not change anything in the analysis proposed here for the labels of the specimens and slides currently held by the Hancock Museum, because those records are completely distinct from the three localities from which we know that Alder and Hancock had specimens. Finally, note that Eliot (1906d) mentioned that he examined a 5/4 mm specimen from the Hancock Museum labeled as "*Doris planata* W.R. Hughes. Sidmouth." According to Eliot, this specimen was completely dry and useless. This specimen, collected by W. R. Hughes from the south coast of England, could not be found: it is probably lost. Eliot (1910b:104) suggested that we regard this specimen as a type: "I have examined the specimen kept in Alder and Hancock's collection at Newcastle labeled "*Doris planata* W. R.Hughes, Sidmouth." It is not the specimen from which the description in the monograph was made, for that animal, we are told, was captured in Lamlash Bay, but it is labeled by Hancock and evidently put in the collection to represent the species, so it must, I think, be regarded as the type specimen." Of course, it is not a type, because it is not the specimen used for the original description.

Type locality.— Lamlash Bay [Isle of Arran, off the western coasts of Scotland]. Contrary to what Eliot (1906d) suggested, Herm Island is not a type locality (see above). Contrary to what Valdés (2002) suggested, Cumbray is not a type locality (see above). Contrary to what Eliot (1910b) suggested, Sidmouth is not a type locality.

Type material condition.— The three slides are well preserved. All radulae present the typical spatulate marginal teeth of *Geitodoris*. The specimen from Herm Island (NEWHM: 2002.H2573) is in fine condition. Its reproductive system, which Eliot (1906d) did not describe, was re-examined and drawn here. The other specimen, from Cumbray, is in poor condition. It probably dried for a while, and is now shapeless.

Distribution.— Mediterranean and eastern European Atlantic.

Discussion.— The anatomy, the taxonomy (including possible synonyms), and the distribution of *planata* will be addressed separately, in a revision of *Geitodoris*. Pruvot-Fol (1936a, 1936b, 1954a) rightly suggested that *Doris testudinaria* Risso, 1818, is a problematic name because its original description could apply to several species. It is regarded here as a *nomen dubium* (see *testudinaria*) despite the fact that Alder (1869) thought that *planata* was just a young *testudinaria*. In the list of references above, only the first publication of new combinations is cited (as well as the references for Alder and Hancock's *testudinaria*, because of their importance for identifying the type material).

Supra-specific relationships.— A phylogenetic test of the relationships of *planata* confirms that *planata* belongs to the clade *Geitodoris*. The Linnaean binomial is *Geitodoris planata*, which is also a possible names under the *ICPN*.

Geitodoris pusae (Marcus, 1955)

Discodoris pusae Marcus, 1955:147-151, figs 151-165.
Geitodoris pusae.— Ortea et al., 1988:243-245, figs 3-10.

Type material.— The original description was based on 12 syntypes that could not be found. A few specimens identified as *Discodoris pusae* were found at the MCZ, from the type locality and from Marcus's collection, but with no collecting date, which prevents us from determining whether those specimens are part of the type material, especially because several other specimens were found at the MCZ, also from the type locality and from Marcus's collection, but collected in 1958, i.e., three years after the original description. However, specimens labeled as types may be found in the future at the MZSP: part of the collection there has not been curated (pers. com., Carlo M. Cunha and Luiz Ricardo L. Simone). Marcus and Marcus (1967a) wrote that they still had 20 specimens of the 'original material.' The latter probably included the 12 syntypes and some additional material collected subsequently from the type locality.

Type locality.— Island of São Sebastião, Brazil.

Distribution.— Western, from Florida to Brazil, although Marcus and Marcus (1969a) recorded *pusae* from temperate waters of the Atlantic coast of Argentina (40°56' S). Ortea et al. (1988) also recorded it from the Canary Islands, eastern Atlantic.

Discussion.— The anatomy, the taxonomy, and the distribution of *pusae* will be addressed separately, in a revision of *Geitodoris*.

Supra-specific relationships.— A phylogenetic test of the relationships of *pusae* confirms that *pusae* belongs to the clade *Geitodoris*. The Linnaean binomial should be *Geitodoris pusae*, which is also a possible name under the *ICPN*.

Geitodoris rubens (Vayssière, 1919) New combination

Discodoris rubens Vayssière, 1919:65-67, plate VI, figs 39-45.

Type material.— Four syntypes (MNHN, no registration number), four specimens 14/7, 13/6, 7/5, and 4/3 mm preserved, [50-70 m depth], [August 1907 and August 1916], leg. A. Vayssière.

Type locality.— [Off] Carry, Golfe de Marseille, [Mediterranean], France.

Type material condition.— The four syntypes, which must have been dry for a while, are currently shapeless and uninformative.

Distribution.— The syntypes are the only specimens known.

Discussion.— The taxonomy of *rubens* will be addressed in detail separately, in a revision of *Geitodoris*, a taxon to which it belongs because of the spatulate outermost teeth of its radula. It is regarded as a *nomen dubium*.

Supra-specific relationships.— A phylogenetic test of the relationships of *rubens* shows that *rubens* belongs to the clade *Geitodoris*. The Linnaean binomial should be *Geitodoris rubens*, which is also a possible name under the *ICPN*.

Geitodoris tema (Edmunds, 1968)

Discodoris tema Edmunds, 1968a:89-93, figs 6-8.
Geitodoris tema.— Schrödl, 2000:208.

Type material.— The holotype, by original designation, was cut in transverse serial sections, deposited at the NHM, London (#19677 W).

Type locality.— One mile east of Tema, Ghana.

Distribution.— The holotype is the only specimens known.

Discussion.— The status of *tema* will be addressed separately, in a revision of *Geitodoris*. Schrödl rightly transferred it to *Geitodoris*.

Aporodoris von Ihering, 1886

Under the *ICZN*, *Aporodoris* is a taxon of genus-level. Type-species: *Doris millegrana* Alder and Hancock, 1854, by monotypy.

The phylogenetic diagnosis of *Aporodoris* includes three main classes of characters, depending on their phylogenetic significance. 1) One synapomorphy exclusively found in this taxon: presence of a membranaceous penial cuticle; only this synapomorophy can be regarded as diagnostic of *Aporodoris* (i.e., only this character can be used to identify that a species belongs to *Aporodoris*). 2) Four synapomorphies of *Discodorididae*: a notched upper lip of the bilabiate anterior foot, digitiform or conical oral tentacles that are *not* expansions of the lateral mouth lips, a flattened prostate divided in two parts of distinct color, and two blood glands. 3) Characters found in many other dorid nudibranchs, e.g., absence of rachidian teeth, hamate lateral teeth, etc.

In the present contribution, *Aporodoris* refers to a clade name, without being assigned to any particular rank. Under the *ICPN*, *Aporodoris* is a converted clade name: it remains an informal clade name until it is phylogenetically defined *and* formally registered. *Aporodoris* could be phylogenetically defined through an apomorphy-based definition as "the clade stemming from the first organism or species to possess a penial cuticle, as inherited by *Aporodoris millegrana* (Alder and Hancock, 1854)."

Aporodoris millegrana (Alder and Hancock, 1854)

Doris millegrana Alder and Hancock, 1854:102-103.
Archidoris millegrana.— Bergh, 1878a: XXXI.
Discodoris millegrana.— Thompson and Brown, 1981:263-266, fig. 1.
Taringa millegrana.— Valdés and Gosliner, 2001:170-173, figs 2F, 47A, 48).
Aporodoris millegrana.— von Ihering, 1886:238-239.
Thordisa ? millegrana.— Bergh, 1894:178.

Type material.— One lectotype (NHM 1980102, one slide) designated by Valdés and Gosliner (2001): one specimen 27/17 mm preserved, leg. Mrs Griffiths, Mus. Leach [according to the original description: "preserved in Dr. Leach's collection in the British Museum"], [no collecting date, before 1854]. One paralectotype (NHM 1980101, two slides and one SEM stub) designated by Valdés and Gosliner (2001): one specimen 25/15 mm preserved, leg. Mrs Griffiths, Mus. Leach [according to the original description: "preserved in Dr. Leach's collection in the British Museum"], [no collecting date, before 1854]. Several labels, preserved in the jars with the specimens, indicate the successive generic affinities proposed: *Doris millegrana* (original binomial), *Aporodoris millegrana* by Eliot in 1910, and *Discodoris millegrana* by Thompson and Brown in 1981. Besides these two type specimens, there was another unlabeled specimen that, according to Thompson and Brown (1981), could possibly be part of the type material. However, this specimen was separated from the two types because Valdés and Gosliner (2001) thought that it did not belong to *millegrana*: this additional specimen could not be examined for the present study. Even if it is a specimen that is not part of *millegrana*, it still part of the type material: it should be a paralectotype (with no name bearing function). The catalogue numbers cited by Valdés and Gosliner (2001) are incorrect: the number for the lectotype is NHM 1980102, not NHM 1980101, and the correct number for the paralectotype is NHM 1980101, not NHM 1980102. All the material available, except for the SEM stub of the notum of the paralectotype (not sent from the NHM) was reexamined. Finally, note that all the anatomical information available (Thompson and Brown 1981; Valdés and Gosliner 2001; present study) is based on the paralectotype.

Type material.— Torquay, [England, English Channel]. Valdés and Gosliner (2001) cited Torbay as the type locality, probably influenced by Thompson and Brown (1981). Although Torbay and Torquay could be regarded as the same locality, Torquay and Torbay designate two different cities, and thus we need to keep Torquay as the type locality, which is the name cited on all the labels of the type material and in the original description.

Type material condition.— The lectotype was partially dissected from the foot. The buccal mass and the reproductive system are missing. Only what is probably the penial membrane is preserved on a slide. The notum is poorly preserved and the nature of the tubercles could not be determined. The paralectotype was entirely dissected by Thompson and Brown (1981). The radula and the labial cuticle are preserved on slides (Thompson and Brown 1981; Valdés and Gosliner 2001). The reproductive system is largely destroyed. Some pieces were illustrated by Valdés and Gosliner (2001). The notum is separated from the foot. A rectangular piece of notum was prepared on a stub for SEM by Valdés and Gosliner (2001).

Distribution.— British Isles (Alder and Hancock 1854), Atlantic coasts of France (Bouchet and Tardy 1976), Mediterranean Sea (von Ihering 1886). Other authors redescribed the types (Eliot 1910b; Thompson and Brown 1981, 1984; Valdés and Gosliner 2001), transferred *millegrana* to a new genus (Bergh 1878a, 1894; Thompson and Brown 1981; Valdés and Gosliner 2001), or just commented on this species (Pruvot-Fol 1954a), with no new material. Note that *millegrana* may be present in the Canaries and in the Mediterranean through some potential junior synonyms (see discussion).

Remarks on the original description.— The original description and the types were already commented on by several authors (Eliot 1910b; Thompson and Brown 1981; Valdés and Gosliner 2001). Here are added a few minor comments. Caryophyllidia are unclear under the microscope, although some of the dorsal tubercles of the paralectotype could be interpreted as caryophyllidia. The SEM picture published by Valdés and Gosliner (2001: fig. 47A) is also not convincing (although the long, narrow tubercles likely are caryophyllidia). There are about 17 rhinophoral lamellae in the lectotype and 15 lamellae in the paralectotype. The labial cuticle is clearly smooth. For the radula, two re-descriptions are already available (Brown 1981; Valdés and Gosliner 2001). The teeth are not redrawn here. Note, however, that the outermost teeth are missing in several rows. Valdés and Gosliner (2001:172-173) "could identify the remainder of the penial armature in one of the microscope slides prepared by Thompson and Brown (1981)." However, they did not draw this penial armature: there is a remainder of what seems to be a penial membrane, but it is largely destroyed.

Discussion.— Valdés and Gosliner (2001) regarded two *Taringa* species names as synonyms of *millegrana*: *Taringa fanabensis* Ortea and Martinez, 1992 (type locality in Tenerife, Canary Islands) and *Taringa tarifaensis* Garcia-Gomez et al., 1993 (type locality in Cadíz, Mediterranean). These synonymies are possible, although they will need to be addressed whenever additional, non-type material is available. Also, the types of *Taringa* species from the Mediterranean and the eastern Atlantic will need to be examined. Importantly, also, the taxonomy of *Aporodoris* in the Mediterranean will require more information about the infra-specific and inter-specific variation of several key features, especially the penial cuticle. This question will require a broad treatment of Atlantic and Mediterranean *Taringa* species. Indeed, several other species names were created for specimens from the Canary Islands, and, in the future, one may want to consider those species names as potential synonyms of *millegrana* (although they could definitely be distinct species): *Taringa ascitica* Ortea, Perez, and Llera, 1981 (described based on a single specimen); *Taringa bacalladoi* Ortea, Perez, & Llera, 1981 (described based on four specimens); *Taringa oleica* Ortea, Perez, & Llera, 1981 (described based on two specimens); *Taringa tritorquis* Ortea, Perez, & Llera, 1981 (described based on three specimens).

SUPRA-SPECIFIC RELATIONSHIPS.— Here, two questions are discussed: 1) the generic affinities proposed for *millegrana*, and 2) the valid name of the clade it belongs to, knowing that *millegrana* is the type species of the genus name *Aporodoris* von Ihering 1886, by original designation.

Bergh (1878a) re-allocated *millegrana* to *Archidoris* and then (Bergh 1894) to *Thordisa* with no explanation. Von Ihering (1886) created a new generic name for *millegrana*, *Aporodoris*. The genus name *Aporodoris* was then used to describe several new species: *Aporodoris rubra* Bergh, 1905; *Aporodoris risbeci* Marcus and Marcus, 1967; and *Aporodoris merria* Burn, 1973. Thompson and Brown (1981) decided to re-allocate *millegrana* to *Discodoris* (Thompson classified all basal discodorids in *Discodoris*). Then, more recently, Valdés and Gosliner (2001) rightly argued that *Aporodoris* von Ihering, 1886, and *Taringa* Marcus, 1955, are two synonyms, and that *millegrana* belongs to *Taringa* species (as shown in the present phylogenetic analysis).

The next question is: Which name should we use for that clade, *Taringa* or *Aporodoris*? The older name, *Aporodoris*, should have priority over the younger name, *Taringa*. Valdés and Gosliner (2001) argued that in this case, however, the *ICZN* Article 23.9 (not 23.9.2) applies and that the younger name should be regarded as valid. However, Article 23.9 actually does not apply here. According to Article 23.9, prevailing usage can be maintained only if two conditions are met (described in 23.9.1), one of which (23.9.1.1) is that the senior synonym must not have been used as a valid name after 1899. Although Valdés and Gosliner (2001) thought that *Aporodoris* had not been used as a valid name since 1899, three new species names were created in *Aporodoris* since 1899 (see above), and several authors used the binomial *Aporodoris millegrana* as valid (Eliot 1910b; Pruvot-Fol 1954a; Bouchet and Tardy 1976). Therefore *Aporodoris* is a valid name, regardless of whether *Taringa* has been widely used or not.

Platydoris Bergh, 1877

Under the *ICZN*, *Platydoris* is a taxon of genus-level. Type-species: *Doris argo* Linnaeus, 1767, by monotypy.

The phylogenetic diagnosis of *Platydoris* includes five main classes of characters, depending on their phylogenetic significance. 1) One synapomorphy exclusively found in this taxon: a flattened body; only this synapomorophy can be regarded as diagnostic of *Platydoris* (i.e., only this character can be used to identify that a species belongs to *Platydoris*). 2) Four synapomorphies of *Discodorididae*: a notched upper lip of the bilabiate anterior foot, digitiform or conical oral tentacles that are *not* expansions of the lateral mouth lips, a flattened prostate divided in two parts of distinct color, and two blood glands. 3) Characters found in many other dorid nudibranchs, e.g., absence of rachidian teeth, hamate lateral teeth, etc. 4) A synapomorphic feature that is not exclusively found in *Platydoris*: the presence of grooved oral tentacles (also a synapomorphy of *Paradoris*). 5) Features that are found in other discodorids but whose phylogenetic significance is still unclear, such as the presence of a distal accessory gland in the reproductive system.

In the present contribution, *Platydoris* refers to a clade name, without being assigned to any particular rank. Under the *ICPN*, *Platydoris* is a converted clade name: it remains an informal clade name until it is phylogenetically defined *and* formally registered. *Platydoris* could be phylogenetically defined through an apomorphy-based definition as "the clade stemming from the first organism or species to possess a flattened body, as inherited by *Platydoris argo* (Linnaeus, 1767)."

***Platydoris ellioti* (Alder and Hancock, 1864)**
Figures 216-217.

Doris ellioti Alder and Hancock, 1864:116-117, plate XXVIII, figs 1-2.
Platydoris ellioti.— Bergh, 1878a: XXVI.— Eliot, 1906b:647-648.— Eliot, 1906c:1003.— Dorgan et al., 2002:284-286, figs 2C, D, 6C, D, 14, 15).

TYPE MATERIAL.— Syntypes (NEWHM 01/09/11; Alder and Hancock's former collection number is 'No 13'): three specimens 45/30, 30/20, and 25/15 mm preserved, leg. Sir Walter Elliot, [no collecting date]. No slides with labial cuticles or radulae could be found at the NEWHM. However, Eliot (1906c:1003) briefly redescribed a radula of *Doris ellioti* from Alder and Hancock's collection, which certainly was extracted from one of the syntypes. If slides are found, they should be numbered 'No 13.'

TYPE LOCALITY.— Madras. Walter Elliot may not have collected his specimens precisely in Madras: see the discussion on the type locality of *fragilis*.

TYPE MATERIAL CONDITION.— The three syntypes were dissected prior to the present study. Only the body walls (dorsal notum and foot) remain: all internal organs are missing. One specimen, probably dried for a while, is hard, which was already the case when Eliot (1906b) re-examined Alder and Hancock's collection. Apparently, Eliot (1906b) was the last one who saw some internal organs (radular teeth and reproductive system) of the types of *ellioti*.

ADDITIONAL MATERIAL EXAMINED.— **Papua New Guinea**, north coast, NW of Madang, Laing Island, Hansa Bay, June 1992, one specimen 75/55 mm preserved, leg. J. M. Ouin, identified as *Platydoris* by T. M. Gosliner (CASIZ 086531) [voucher of *Platydoris ellioti* by Dorgan et al. (2002); this specimen was dissected prior to the present study; a piece of notum was prepared for SEM].

DISTRIBUTION.— Madras (type locality) and Papua New Guinea (Dorgan et al 2002). Additional, uncertain localities are (see discussion): Indonesia (Abraham 1877, as *Doris speciosa*), Ceylon (Farran 1905, as *Platydoris speciosa*), Japan (Baba 1949, as *Argus speciosus*), New Caledonia (Risbec 1928, as *Kentrodoris pseudofusca*), and the Philippines (Dorgan et al. 2002, as *Platydoris sabulosa*). The specimens described as *Discodoris ellioti* and *D. ellioti* var. by Bergh (1905) are no part of *ellioti* (see discussion). Finally, note that Pruvot-Fol (1954b) described a specimen that she identified as *Austrodoris ellioti* (Alder and Hancock, 1864), which is actually part of *nubilosa* (see this species).

REMARKS ON THE ORIGINAL DESCRIPTION (Fig. 216).— The color of live specimens was described as follows: "Yellowish colour, inclining to orange, thickly spotted with umber-brown, the spots larger towards the sides, and margin surrounded by thick-set purplish-brown blotches; the extreme edge pale: underside yellowish orange, with large dark brown circular spots, intermingled with a few smaller and lighter ones; the margin blotched with brown." The current color of the preserved specimens is homogenously creamish-greenish, with no blotches or dots. The specimens are flattened, with a narrow pedal sole. The oral tentacles are small, conical and deeply grooved (instead of simply linear, as described by Alder and Hancock). The margin of the gill opening is distinctly lobed, as in other *Platydoris* species. The numerous flat tubercles of the dorsal notum are poorly preserved but are most likely caryophyllidia. Alder and Hancock did not provide any anatomical data, but Eliot (1906b, 1906c) commented on the type material and described briefly both the reproductive system and the radula. Eliot's comments (1906b, 1906c) are particularly valuable because no internal organs (lost or kept by Eliot?) remain: the labial cuticle is smooth; the radular formula is 40 × (100-0-100); the rachis is narrow; "the outermost of all [teeth] sometimes bears a few irregular denticulations. The ramaining teeth are hamate, erect, and fairly strong;" Eliot also described the spines usually found in the genitalia of *Platydoris*, although he could not determine whether those spines were in the vagina or the deferent duct.

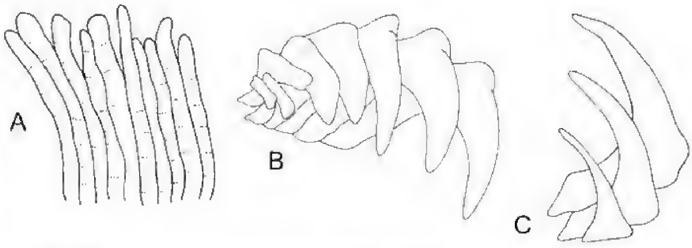

FIGURE 216. *Platydoris elliotii*, after Bergh (1905: plate XV). A. Jaw rodlets (fig. 6).— B. Outermost teeth (fig. 8a).— C. Outermost teeth, *Platydoris elliotii* var. (fig. 9).

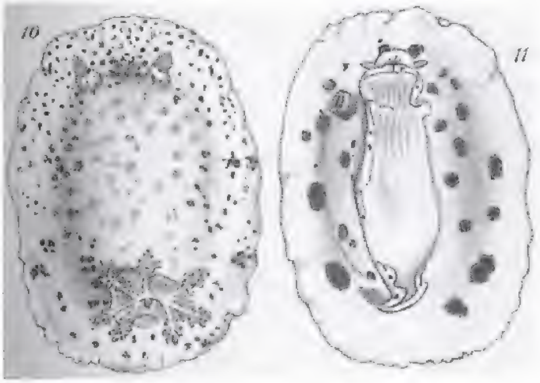

FIGURE 217. *Platydoris elliotii*. Dorsal and ventral surface, original description of *Doris speciosa* (Abraham 1877: plate 28, figs 10-11).

DISCUSSION.— The literature on *elliotí* needs to be commented on. It was first re-allocated from *Discodoris* to *Platydoris* by Bergh (1878a) with no discussion, in a checklist of species names. Later on, Bergh (1905) described one 50/35 mm specimen from Makassar (South Sulawesi, Indonesia) as *Discodoris elliotí* (then a new combination) and another 80/45 mm specimen from Ruma-Kuda-Bai, Roma Island (Indonesia), as a variety of *Discodoris elliotí*. However, it is likely that those two specimens (which could not be found at the ZMUC) are not part of *elliotí* because Bergh described jaws on the labial cuticle (and the labial cuticle of *Platydoris* species is smooth); also, Bergh did not mention some of the distinct features of *Platydoris*, such as the six-lobed margin of the gill opening and the deeply grooved oral tentacles. Bergh was probably looking at some basal discodorids (in fact he mentions *Discodoris concinna* at the end of his description), which might explain why he placed *elliotí* in *Discodoris* instead of *Platydoris*, as he had correctly done in 1878.

At the same time, Farran (1905) described a few species from Ceylon, including specimens that he identified as *Platydoris inframaculata* (Abraham, 1877) and *Platydoris speciosa* (Abraham, 1877). Interestingly, he pointed out in his discussion of his description of the 57/45 mm specimen identified as *speciosa* that *inframaculata* and *speciosa* could be synonyms of both the *Doris elliotí* and *Doris formosa* of Alder and Hancock. However, he recognized that this could not be determined without examination of animals in their "natural colors." The synonymy of *elliotí* with *formosa* is unlikely though, given the description of scarlet dots on the dorsal notum in the original description (see, Dorgan et al. 2002: fig. 6E). Farran described the color of his *speciosa* specimen as follows [it is unclear whether it is a description based on Dr. Herdmann's notes, as in some other species, or just the preserved specimen; however, it could be based on Dr. Herdmann's notes because, in other species, he sometimes mentions that he described the color of the 'spirit' specimen]: "The ground colour of the specimen is an opaque muddy brownish-grey. The mantle is marked above with collections of small, purplish-brown spots, irregularly placed over the whole surface. The lower sides of the mantle are marked with large, purple-brown, circular blotches, with smaller ones on the side of the body." It is clear (based on his description of the reproductive system and of the external morphology) that Farran looked at some *Platydoris* specimens. Now, whether or not he actually looked at specimens of *speciosa* is more difficult to determine because Abraham's (1877:250-251, plate XXVIII, figs 10-11; here Fig. 217) original description of *speciosa* only indicated that the "spirit specimen [was] light brownish, closely and irregularly blotched with reddish brown on the back. (...) underneath, the general tint is yellowish brown with an orange tinge upon the foot, and with a few large unequal round or oval black spots upon the sides of the body and upon the neighboring portion of the mantle; some smaller spots are upon the sides of the foot." It seems that Farran's identification of specimens as *speciosa* was more based on a general similarity than on the sharing of a diagnostic feature. Therefore, his identification is regarded here as hypothetical. This interpretation makes sense because Farran himself recognized that it was not possible to distinguish clearly *speciosa* from *inframaculata*, *ellioti*, and *formosa*.

A year later, in 1906, Eliot (1906b, 1906c) re-examined the type material of *ellioti* and commented on it (see above). He also wrote that placing *ellioti* within *Discodoris* (as Bergh did in 1905) was inaccurate (he favored the combination *Platydoris ellioti*), but did not write that the specimens that Bergh identified as *ellioti* were probably not part of *Platydoris*.

Baba (1949:153-154, plate XXVI, fig 96) described from Sagami Bay some specimens of *Argus speciosus* (Abraham), a "very common" species on the Pacific coasts of Japan from Bôshû southwards." Based on his description, Baba clearly dealt with *Platydoris* specimens. He described their color as follows: "Ground color of back brown, covered irregularly with bold, cloud-like blotches of chocolate, and the whole back is sprinkled with deeper chocolate spots. Rinophores dark yellow, branchial plumes dark brown. Underside of mantle with a series of round or oval markings of chocolate, which are conspicuous on the orange-yellow background. Sole orange-yellow."

Then Dorgan and co-authors (2002) described a specimen (CASIZ 086531; re-examined here) as *Platydoris ellioti*. For the distribution of *ellioti*, they gave: India (Alder and Hancock 1864), Japan (Baba 1949), New Caledonia (Risbec 1928), and Papua New Guinea (their study). The color pictures provided by Dorgan et al. (2002: figs 2C-D) could fit with the original description of *ellioti*, so the specimen they identified as *ellioti* may be part of *ellioti*. Dorgan et al. accepted two synonymies without discussing them – *Kentrodoris pseudofusca* Risbec, 1928, with type locality in New Caledonia, and *Platydoris speciosa* (Abraham, 1877), type locality in Amboina, would both be synonyms of *ellioti*. Also, Dorgan et al. created a new species name, *Platydoris sabulosa*, for a single specimen whose anatomy is close to that of *ellioti*, without considering the possibility of infra-specific variation, examining the type material of *ellioti*, nor citing the re-description of the type material of *ellioti* by Eliot in 1906. Which specimens can be regarded as real *ellioti*, and which synonymies can we accept?

Generally speaking, it is difficult to make a decision based on vague descriptions of the dorsal color. For example, the description of the color of the type (by monotypy) of *speciosa* by Abraham is based on a "spirit" specimen, which means that we have basically no idea of what the live animal looked like. Therefore, it is difficult to determine whether or not *speciosa* is a synonym of *ellioti*. If *speciosa* is a synonym of *ellioti*, as claimed by Dorgan and co-authors, then Amboina (Indonesia) should be added to the distribution. The reader is free to decide whether the specimen from Ceylon described as *Platydoris speciosa* by Farran is part of *speciosa* and/or *ellioti* (through synonymy or misidentification). Now, is the *speciosus* specimen described by Baba in 1949 part of *ellioti*? If, as claimed by Dorgan and co-authors, it is part of *ellioti* (through synonymy), then the dorsal notum of *ellioti* shows a high variation in darkness/brightness: indeed, the color drawing provided by Baba (1949: plate XXVI, fig. 96) illustrates a dorsal notum that is much darker than the picture published by Dorgan et al. (2002: fig. 6C).

Is *Kentrodoris pseudofusca* Risbec, 1928, a synonym of *ellioti*? The original description, based on a single 120 mm long specimen from New Caledonia, is confusing: Risbec describes that the edges of the mantle are lobed and can break easily, which is a feature usually found in *boholiensis*, and not in *Platydoris*; Risbec does not write a single word about the penial and vaginal spines.

However, the branchial margin is lobed and the specimen could be a *Platydoris* (although this feature is also found in *Asteronotus*). The color drawing provided by Risbec (1928: plate III, fig. 2) of the dorsal notum (light brown background with darker blotches and spots) appears to be compatible with the color picture of Dorgan et al. (2002: fig. 6C), especially because Risbec describes the ventral color as "dark orange with rounded, dark, purple blotches." However, this similarity is not strong: Risbec's (1928: plate III, fig. 2) drawing for *pseudofusca* differs greatly from Baba's (1949: plate XXVI, fig. 96) drawing for *speciosa* (i.e., *ellioti*, according to Dorgan et al.); thus, if *pseudofusca* were to be accepted as a synonym of *ellioti*, then, again, the dorsal color would present a great deal of variation.

Finally, is *Platydoris sabulosa* Dorgan, Valdés, and Gosliner, 2002, distinct from *ellioti*? According to these authors: "*Platydoris sabulosa* resembles *P. ellioti* in the presence of large ventral spots, but its coloration is more uniformly tan. Internally, these two species are clearly distinguishable by the reproductive system and radular morphology. The prostate and the accessory gland of *P. ellioti* are always much larger than those of *P. sabulosa*. The relative size of the receptaculum seminis compared with the bursa copulatrix is much larger in *P. sabulosa* than in *P. ellioti*. The mid-lateral teeth of *P. ellioti* have a long, curved cusp, being straight and shorter in *P. sabulosa*. The outermost teeth are longer and more curved in *P. sabulosa* than in *P. ellioti*." Such comparison looks fine, except that it is based exclusively on two specimens, one for each species. Therefore, it is difficult to know whether the differences mentioned are due to individual variation or actual specific differences (and, for instance, the present study demonstrates that the relative size of spermatic pouches varies a great deal). Also, the striking color variation found between Baba's drawing (1949: plate XXVI, fig. 96) for a specimen regarded as part of *ellioti* by Dorgan and coauthors, and the color picture of *ellioti* by these authors (2002: fig. 6C) might indicate that the dorsal color could vary within *ellioti*, explaining the pattern found in *sabulosa*. There might be two species (*ellioti* and *sabulosa*), but the single specimen described as *sabulosa* could have been interpreted as a variant of *ellioti* instead of a distinct species: more specimens are needed.

In summary, let us accept here the presence of *ellioti* in Madras (type locality) and Papua New Guinea (Dorgan et al. 2002), with additional but hypothetical localities in Indonesia (Abraham 1877, as *Doris speciosa*), Ceylon (Farran 1905, as *Platydoris speciosa*), Japan (Baba 1949, as *Argus speciosus*), New Caledonia (Risbec 1928, as *Kentrodoris pseudofusca*), and the Philippines (Dorgan et al. 2002, as *Platydoris sabulosa*).

Supra-specific relationships.— A phylogenetic test of the relationships of *ellioti* confirms that *ellioti* belongs to *Platydoris*. The Linnaean binomial for *ellioti* should remain *Platydoris ellioti*, which is also a possible name under the *ICPN*.

Platydoris sibogae (Bergh, 1905)

Figure 218.

Discodoris sibogae Bergh, 1905:248, plate I, fig. 8.
Platydoris sibogae.— Lim and Chou, 1970:101, figs 1V, 10D.

Type material.— The type material could not be found. It is neither at the ZMA, with the other specimens from the Siboga Expedition, nor at the ZMUC, with Bergh's collection. It is probably lost. Also, we ignore how many specimens Bergh referred to as *Discodoris sibogae*: the latter is available because of an illustration (which is an indication, not a description, ICZN Article 12.2, 12.2.7).

Type locality.— The type locality is unknown.

Distribution.— This species is only known from the type material, as well as four specimens from Singapore identified as *Platydoris sibogae* by Lim and Chou (1970). *Platydoris sibogae*, however, is a junior synonym of *Platydoris scabra* (Cuvier, 1804), which is distributed throughout the tropical Indo-West-Pacific (see below).

Discussion.— The original description of *Discodoris sibogae* needs to be commented on. Indeed, the description provided by Bergh (1905:104-106) for *Discodoris* ? *sibogae* is not the description of *Discodoris sibogae*. Bergh (1905:248) clearly stated in his *corrigenda*, on the last page of text of his volume on the Siboga opisthobranchs, that the description of *Discodoris* ? *sibogae* actually was the description of *Discodoris rubra*, another new species. Bergh's *corrigenda* also tells us that the figure that illustrates the dorsal color of *Discodoris sibogae* is Bergh's figure 8 (1905: plate 1, fig. 8), and the figure that illustrates the dorsal color of *Discodoris rubra* is Bergh's figure 7 (1905: plate 1, fig. 7). The species *Discodoris sibogae* (with *no* question mark) then did not have any description. The page number for *Discodoris sibogae* is page 248, i.e., the page number of the *corrigenda*, where it appears with no question mark, and with no mention of '*sp. nov.*' This species name is not a *nomen nudum* because it was published before 1930, and the illustration can be regarded as an indication (*ICZN*, Article 12.2, 12.2.7). However, note that the only information we have for *Discodoris sibogae*, besides the name, is a drawing of the dorsal color, which, after all, is better than what we have for many descriptions!

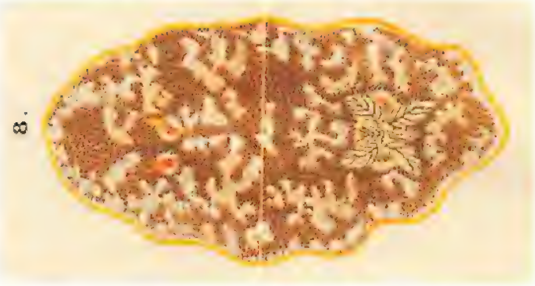

Figure 218. *Platydoris sibogae*. Dorsal color, original description of *Discodoris sibogae* (Bergh, 1905: plate I, fig. 8).

The status of *Discodoris sibogae* was discussed in two publications (Lim and Chou 1970; Dorgan *et al.* 2002). In both cases, the authors overlooked the fact that Bergh's written description of *Discodoris* ? *sibogae* was the description of *Discodoris rubra* (illustrated on plate 1, fig. 7), and not that of *Discodoris sibogae* (illustrated on plate 1, fig. 8). However, in both cases, the authors attached the specific name *sibogae* to the correct figure, i.e., Bergh's figure 8, on plate 1.

Lim and Chou (1970), who described four specimens of *Platydoris sibogae* from Singapore, Malaysia, regarded *Platydoris sibogae* as a valid name.

Dorgan and co-authors (2002), who overlooked Lim and Chou's paper, argued that *Discodoris* ? *sibogae* was a synonym of *Platydoris scabra* (Cuvier, 1804). By "*Discodoris ? sibogae*," Dorgan et al. (2002) referred to "*Discodoris ? sibogae* Bergh, 1905:104–106, pl. 1, fig. 8," i.e., the wrong written description and the wrong page numbers (it should be page 248, because pages 104-106 actually are the description of *Discodoris rubra*). However, Dorgan et al. (2002:279) rightly pointed out that Bergh's figure 8 (Bergh 1905: plate 1, fig. 8) illustrates the dorsal color of a specimen similar to *Platydoris scabra*, especially the thin yellowish line along the margin of the notum.

Jorunna Bergh, 1876

Under the *ICZN*, *Jorunna* is a taxon of genus-level. Type-species: *Jorunna johnstoni* (Alder & Hancock, 1845), by monotypy, which is regarded as a synonym of *Jorunna tomentosa* (Cuvier, 1804).

The phylogenetic diagnosis of *Jorunna* includes four main classes of characters, depending on their phylogenetic significance. 1) One synapomorphy exclusively found in this taxon: distal accessory gland in the reproductive system with a long stylet in it; only this synapomorophy can be regarded as diagnostic of *Jorunna* (i.e., only this character can be used to identify that a species belongs to *Jorunna*). 2) Four synapomorphies of *Discodorididae*: a notched upper lip of the bilabiate anterior foot, digitiform or conical oral tentacles that are *not* expansions of the lateral mouth lips, a flattened prostate divided in two parts of distinct color, and two blood glands. 3) Characters found in many other dorid nudibranchs, e.g., absence of rachidian teeth, hamate lateral teeth, etc. 4) Features that are found in other discodorids but whose phylogenetic significance is still unclear, such as the presence of caryophyllidia on the dorsal notum.

In the present contribution, *Jorunna* refers to a clade name, but is not assigned to any particular rank. Under the *ICPN*, *Jorunna* is a converted clade name: it remains an informal clade name until it is phylogenetically defined *and* formally registered. *Jorunna* could be phylogenetically defined through an apomorphy-based definition as "the clade stemming from the first organism or species to possess a flattened body, as inherited by *Jorunna tomentosa* (Cuvier, 1804)."

A revision of *Jorunna* was recently published (Camacho-García and Gosliner 2008), which showed that *Kentrodoris* is nested within *Jorunna*.

Jorunna whitleyi (Allan, 1932) New combination

Discodoris whitleyi Allan, 1932:88-89, plate IV, figs 1-2.

Type material.— Holotype (AM C57205), by original designation: one specimen 40/16 mm alive, leg. A. W. G. P. Whitley, May 1931. The holotype, requested, could not be borrowed.

Type locality.— North West Islet, Capricorn Group, Queensland.

Distribution.— Two specimens are known, both from the type locality.

Remarks on the original description.— The color of the live animal was described as "yellowish cream, with irregular sized patches of dark brown color scattered over the whole of the dorsal surface. These patches, which are smaller, though more numerous towards the margins, are composed of stipulations of dark colour, and are easily rubbed off in the preserved specimens." The color of the rhinophores was also described: "The club-shaped portion of the rhinophores is rich black, and the lower portion whitish." The animals were elongate-oval. Allan distinctly described a notched upper lip of the anterior foot and digitiform oral tentacles. The branchial sheath was not divided in lobes. The dorsal surface was covered with "minute granulations, which [were] inclined to rub off in the preserved specimen." It is difficult to determine whether those granulations are caryophyllidia or not. The internal anatomy was not described.

Discussion.— The original description is largely incomplete. However, the drawing of the dorsal surface provided by Allan suggests that *whitleyi* could be a synonym of *Jorunna funebris* (Kelaart, 1858), common in the tropical Indo-West Pacific, with which it shares a similar dorsal color, including the rhinophores (black with a white peduncle). This synonymy will have to be confirmed through the re-examination of the type.

Jorunna annuligera (Bergh, 1876)

Kentrodoris annuligera Bergh, 1876:423-427, plate XLI, fig. 1, plate LII, figs 3-16.
Discodoris annuligera.— Lim and Chou, 1970:99, 104, figs 1F, 3F, 4L, 7A-B.

Type material.— The two syntypes could not be found at the ZMUC, which holds, however, a slide with a radula.

Type locality.— Philippines (Samar) and Palau (Aibukit)

Distribution.— Tropical Indo-West Pacific (mainly as *funebris*)

Discussion.— *Kentrodoris annuligera* is regarded by most current authors (see Marcus 1976b) as a junior synonym of *Kentrodoris funebris* (Kelaart, 1858). Lim and Chou (1970) first identified several Malaysian specimens as *Discodoris* sp., and then, in the addendum of the same article (Lim and Chou 1970:104), wrote that their correct identification was *Discodoris annuligera* (Bgh.). The species identification is correct: their specimens are part of *annuligera*. However, Lim and Chou did not explain why they decided to re-allocate *annuligera* from *Kentrodoris* to *Discodoris*. *Jorunna* is used here as the first part of the binomial, in agreement with the recently-published revision of *Jorunna* (Camacho-García and Gosliner 2008).

Hiatodoris Dayrat, 2009, New name

Based on the supra-specific relationships found, a new supra-specific name is proposed, *Hiatodoris*, a new genus name under the ICZN and an unranked, new clade name under the *ICPN*. The etymology of *Hiatodoris* is '*hiatus*,' which means 'gap' in Latin, and refers to the empty space in the rachidian region of the radula. *Hiatodoris* possesses all the synapomorphies of *Discodorididae*, which are plesiomorphic at its level and thus are not diagnostic of *Hiatodoris* only: notched upper lip of the bilabiate anterior foot; digitiform oral tentacles; flattened prostate divided in two (proximal and distal) parts; and two blood glands. However, *Hiatodoris* can be distinguished from other discodorids based on a radular feature that is diagnostic because it is a synapomorphy of *Hiatodoris*, and it is only known in *Hiatodoris*: the radula is characterized by a large, empty rachidian space in between the two lateral sides of the radula. Note, however, that this feature was found in only a few specimens available.

Under the ICZN, the type species of *Hiatodoris* is *Peltodoris fellowsi* Kay and Young, 1969. *Hiatodoris* currently includes two caryophyllidia-bearing species, *fellowsi*, from the tropical West Pacific, and sp. B, an unnamed species described here, endemic to the Galapagos Islands.

Under the *ICPN*, *Hiatodoris* is a new clade name that could be phylogenetically defined through an apomorphy-based definition as 'the clade stemming from the first organism or species to possess a radula with a wide, empty rachidian space in between the two lateral side, as inherited by *Hiatodoris fellowsi* (Kay and Young, 1969).'

Hiatodoris fellowsi (Kay and Young, 1969), New combination

Figures 219-222.

Peltodoris fellowsi Kay and Young, 1969:197, figs 36-37.— Kay, 1979:466, fig. 149D.— Bertsch and Johnson, 1981:42, unnumbered figure.— Edmunds and Preece, 1996:413.— Debelius, 1996:248.— Hoover, 1998:172, unnumbered figure.

Discodorididae fellowsi.— Dayrat and Gosliner, 2005:205.

TYPE MATERIAL.— Kay and Young deposited a holotype and three paratypes at the B. P. Bishop Museum, Honolulu, Hawaii. One paratype (BPBM 8922) was borrowed and dissected for the present study: one specimen 34/24 mm preserved, Oahu, Pupukea, [10 meters depth], [leg. D. Fellows, or A. Kay and D. Young, the label indicates no collector, but probably collected by Kay and Young because the specimen collected by D. Fellows has the catalogue number BPBM 8921 and was collected in July 1965], July 1966 [according to the publication, the specimens were collected in July 1965, and in May and October 1966].

TYPE LOCALITY.— Pupukea, Oahu, Hawaii.

TYPE MATERIAL CONDITION.— The paratype borrowed (BPBM 8922) was complete and in good condition.

ADDITIONAL MATERIAL DISSECTED.— **Hawaii**, Maui, Black Rock, 4 meters depth, 6 May 2003, one specimen 25/17 mm preserved, leg. Cory Pittman, identified as *Discodoris fellowsi* by Cory Pittman (CASIZ 166765).

Distribution.— West Pacific: Hawaii, probably New Caledonia (see below, *www*) and warm Japanese waters (see below, *www*), and hypothetically Pitcairn. Kay and Young mentioned a total of five specimens from the type locality. Bertsch and Johnson (1981), Hoover (1998) and Debelius (1996) published pictures of additional specimens from Oahu. Maui (present study) is a new record for the Hawaiian Islands. The presence of *fellowsi* in Henderson Island, Pitcairn Group, based on two specimens identified by Edmunds and Preece (1996) needs to be confirmed (see discussion).

Literature.— So far, only Kay and Young (1969) have provided anatomical observations. Pictures of live animals can be found in several field guides (Kay 1979; Bertsch and Johnson 1981; Debelius 1996; Hoover 1998).

WWW.— Two interesting new records were presented recently on Bill Rudman's *Sea Slug Forum*. One specimen was collected at Lifou, Loyalty Islands, during the international workshop organized by the Muséum national d'histoire naturelle, in November 2000 (*Sea Slug Forum*, 23 January 2001, #3661). Hideyuki Takasu found several specimens in warm Japanese waters, at Hachijo Island (*Sea Slug Forum*, 30 January 2001, #3622). The color of those specimens is similar to the specimens known from Hawaii (white ground color, black rhinophores and gills). However, Bill Rudman rightly suggests that those identifications would need to be verified with anatomical observations.

Occurence.— So far, at least seven specimens were mentioned from Hawaii (Kay and Young 1969; Bertsch and Johnson 1981; Debelius 1996; Hoover 1998; present study), one from Lifou, Loyalty Islands (*Sea Slug Forum*), several from warm Japanese waters (*Sea Slug Forum*), and two from Henderson Island (Edmunds and Preece 1996). It does not seem that *fellowsi* is common.

Habitat.— In dead coral (Kay and Young 1969), on wall (CASIZ 166765), in caves and ledges in 10-15 meters of water (Bertsch and Johnson 1981), seaward side of reef crest (Edmunds and Preece 1996),

Etymology.— For David Fellows, who "collected a specimen" (Kay and Young 1969:197).

Remarks on the original description (Figs. 219A-B).— The "numerous fine granules" described by Kay and Young (1969:197) on the mantle are caryophyllidia. The color is well preserved: white mantle with black rhinoporal lamellae (15), red-brown rhinophoral peduncles, black gills (6) except for the red-brown rachis. The oral tentacles are digitiform and the upper lip of the anterior foot is notched. The labial cuticle is smooth. The radular formula is 23 × (24-0-24). All teeth are hamate. Kay and Young (1969:197) described that: "A short uterine duct passes from the spermatocystic duct to the junction of the ampullary duct and prostate at the albumin and mucous gland." This is unexpected because the so-called uterine duct (i.e., fertilization duct) connects to the fertilization chamber. Of course, if the female duct (which carries the ovocytes from the ampulla to the fertilization chamber and then carries the fertilized eggs from the fertilization chamber to the genital opening through the albumen and mucous glands) is short, then the fertilization chamber is close to the point where the female duct and the male duct separate. However, this area is extremely difficult to observe by dissection: it was only exceptionally seen in the context of the present monograph.

Description of new specimens (including paratype BPBM 8922, Figs. 219C-E, 220-222).— *Color*. The color of live animals was homogeneously white on both the ventral and the dorsal surface, except for the gills and the rhinophores that are black. This pattern could also be observed in preserved specimens.

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform and not grooved. The dorsal notum bears tubercles that are caryophyllidia. Only a few small holes of which the diameter is less than 10 μm as well as a few tufts of cilia could be observed, probably due to the preservation. In preserved specimens, the margins of the rhinophoral and branchial sheaths can be smooth or lightly crenulate. There are six tripinnate branchial plumes arranged in circle around the anus. The branchial sheath presents five or six shallow lobes in one preserved specimen (BPBM 8922), but not as deep as in *Platydoris*. The rhinophores have from 15 to 20 lamellae.

Digestive system. The stomach is free, narrow, and median (paratype). No caecum could be observed. The intestine is straight and dorsal. The labial cuticle is smooth. The length of the radula equals twice its width if the rachis is taken into account, but almost four times its width if the rachis is not considered. The radular sac can (CASIZ 166765) or cannot (BPBM 8922) be seen by dorsal dissection. The radular formulae are: 24 × (21-0-21) in a 34 mm long specimen (BPBM 8922), and 24 × (20-0-20) in a 25 mm long specimen (CASIZ 166765). The rachidian teeth are absent. The rachidian space is as wide as each lateral side of the radula. The lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the teeth gradually increases from the first innermost tooth to the tenth lateral tooth, then stays approximately constant, and finally decreases with the last two or three innermost teeth (BPBM 8922). In the other specimen (CASIZ 166765), the size of the teeth gradually increases from the first innermost tooth to the tenth lateral tooth, and then gradually decreases up to the vestigial outermost teeth. All the teeth are hamate. Outermost teeth are fully hamate (BPBM 8922) or reduced (CASIZ 166765). The teeth bear no denticles, nor are they grooved.

Nervous system. The circum-esophageal nerve ring is short, i.e., its length equals approximately twice the width of the two dorsal cerebro-pleural ganglia. The cerebral and pleural ganglia are completely fused.

Reproductive system. The ampulla is straight. The division between male and female ducts could not be seen by dissection. The prostate is divided in a proximal yellowish part and a distal orange part. Both parts are easily recognizable. The deferent duct is straight (BPBM 8922) or loosely convoluted with a short loop (CASIZ 166765). No distal accessory gland and no distinct penial papilla were found. The vaginal duct is straight; the fertilization duct is straight too. The connection between the fertilization duct and the female gland mass is not marked by a distinct duct and the duct of the receptaculum seminis seems to be the prolongation of the fertilization duct. The bursa copulatrix is as large as (CASIZ 166765) or almost twice (BPBM 8922) as large as the receptaculum seminis. The spermatic pouches are ovate and closely attached to one another.

DIAGNOSTIC FEATURE.— The white ground color of the dorsal notum with black rhinophores and gills is a distinct pattern that can hardly be confused with any other discodoridid species. In addition, the organization of the reproductive system and the radula may be useful if some unexpected variation is found for the color, such as the presence of ocelli (Edmunds and Preece 1996).

INFRA-SPECIFIC CHARACTER VARIATION.— The radular formulae found in the present study are congruent with the formula described originally by Kay and Young, 23 × (24-0-24). However, the radular formulae are expected to vary when smaller and larger specimens are dissected. Kay and Young illustrated a "loosely convolute" vaginal duct and a "tightly convolute" deferent duct: however, this sort of infra-specific variation (the ducts observed here were loosely convoluted) is common.

DISCUSSION.— The color is distinctive. Additional black ocelli on the dorsal surface were mentioned only in specimens from Pitcairn (Edmunds and Preece 1996). The presence of *fellowsi* in Pitcairn still needs to be verified in the future: one will have to address whether black ocelli are due to individual variation or incompatible with *fellowsi*.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *fellowsi* shows that *fellowsi* does not belong to *Peltodoris*, but rather belongs to a clade that also includes sp. B (an

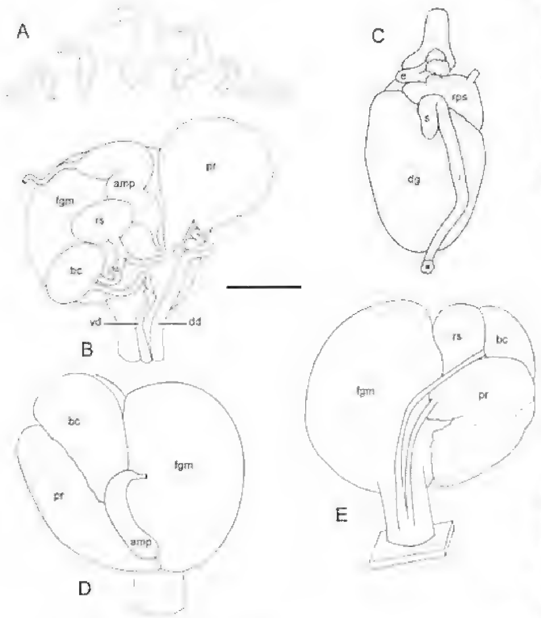

FIGURE 219. *Hiatorodoris fellowsi*. A. Radular teeth, after Kay and Young (1969: fig. 36).— B. Reproductive system, after Kay and Young (1969: fig. 36).— C. General anatomy, paratype (BPBM 8922), scale = 6 mm.— D. Reproductive system, paratype (BPBM 8922), scale = 3 mm.— E. Reproductive system, paratype (BPBM 8922), scale = 3 mm.

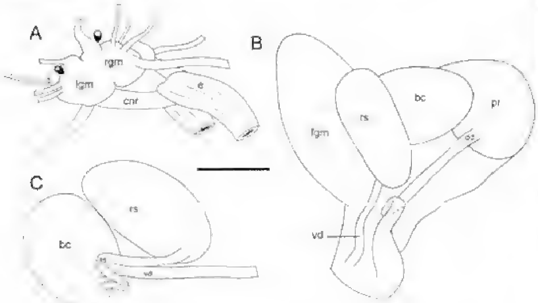

FIGURE 222. *Hiatorodoris fellowsi*, CASIZ 166765. A. Nervous system, scale = 1.2 mm.— B. Reproductive system, scale = 1 mm.— C. Spermatic pouches, scale = 0.3 mm.

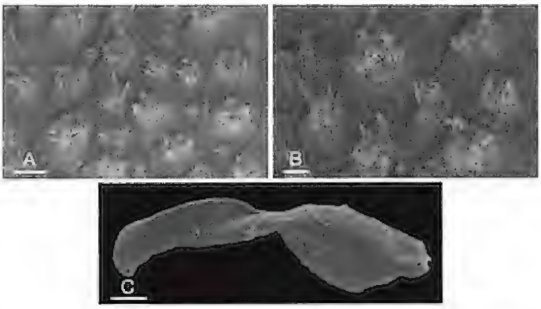

FIGURE 220. *Hiatorodoris fellowsi*, notum and penial papilla. A. Dorsal notum, caryophyllidia, paratype, BPBM 8922, scale = 100 µm.— B. Dorsal notum, caryophyllidia, paratype, BPBM 8922, scale = 60 µm.— C. Penial papilla, CASIZ 166765, scale = 100 µm.

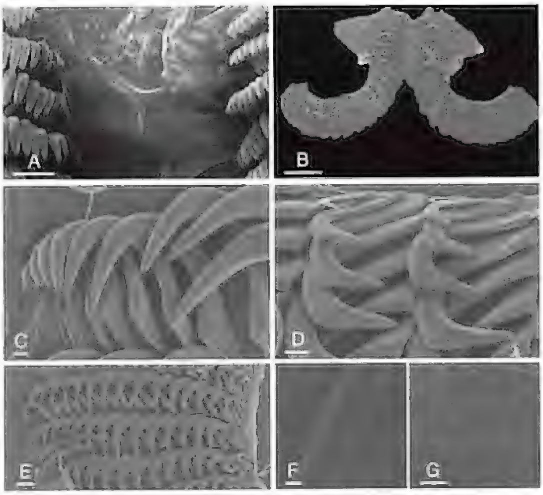

FIGURE 221. *Hiatorodoris fellowsi*, labial cuticle and radula. A. Rachidian space, paratype, BPBM 8922, scale = 200 µm.— B. Radula, CASIZ 166765, scale = 1 mm.— C. Innermost teeth, CASIZ 166765, scale = 20 µm.— D. Outermost teeth, CASIZ 166765, scale = 40 µm.— E. Right rows, CASIZ 166765, scale = 100 µm.— F. Smooth labial cuticle, paratype, BPBM 8922, scale = 30 µm.— G. Smooth labial cuticle, CASIZ 166765, scale = 100 µm.

unnamed, new species described here): both species have a similar radula, which also is distinct from other discodorids. A new taxon name (new genus name under the ICZN) is created for this clade, *Hiatodoris*, with *Peltodoris fellowsi* as the type species (under the ICZN). The new valid name for *Peltodoris fellowsi* should be *Hiatodoris fellowsi*, which is also a possible name under the *ICPN*.

Hiatodoris sp. B, new and unnamed species

Figures 223-226.

Discodoris sp. Debelius, 1996:247, unnumbered figure.— Hickman and Finet, 1998:126, unnumbered figure.
Diaulula sp. Camacho-García et al., 2005:86, unnumbered figure.

MATERIAL DISSECTED.— [**Eastern Pacific Ocean**], Ecuador, Galapagos Islands, Isla Fernandina, 27 meters depth, 1993, one specimen 35/25 mm preserved, leg. Paul Humann, identified as *Discodoris* by T. M. Gosliner (CASIZ 088588) [this specimen was dissected prior to the present study: the buccal mass could not be found when the present work was conducted but the radula is available on a stub in the CASIZ collection (T. M. Gosliner); a piece of notum was cut]; Ecuador, Galapagos Islands, Isla Fernandina, North side, 15 May 1994, one specimen 17/10 mm preserved, leg. R. J. Van Syoc aboard Mistral II, identified as *Discodoris* by T. M. Gosliner (CASIZ 097537).

DISTRIBUTION.— Galapagos Islands.

LITERATURE.— Color pictures have been published in field guides (Debelius 1996; Hickman and Finet 1998; Camacho-García et al. 2005).

DESCRIPTION (Figs. 223-226).— *Color.* The background of the dorsal notum is yellow, with dark, irregular (almost circular) spots. Preserved specimens are creamish, with still distinct spots on the dorsal notum and the hyponotum, but not on the foot sole.

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform and not grooved. The dorsal notum bears tubercles that are caryophillidia (although the notum was poorly preserved). There are six tripinnate branchial plumes. Rhinophoral lamellae could not be counted.

Digestive system. The stomach is free, on top of the left anterior side of the digestive gland. A small caecum is present. The intestine is straight and dorsal. The labial cuticle is smooth. The radular sac cannot be seen by dorsal dissection. The radular formula is 18 × (40-0-40) in a 17 mm long specimen (CASIZ 097537). Rachidian teeth are absent. The rachidian area equals about one third of the total width of the radula, and bears approximately ten innermost lateral teeth that are significantly smaller than the rest of the teeth. Those small, innermost teeth are only present in a few rows in the anterior half of the radula. The size of the lateral teeth is globally constant, except for the innermost teeth that are significantly smaller, and the last four or five outermost ones of which the size decreases gradually. All teeth are hamate, ungrooved; they bear no denticles.

Nervous system. The circum-esophageal nerve ring is short. The cerebral and pleural ganglia are fused. The surface of the ganglia is smooth.

Reproductive system. The ampulla is loosely convoluted. The division between male and female ducts (in the female gland mass) could not be seen by dissection. The flattened prostate is divided in a proximal whitish part and a distal yellowish part. The deferent duct is straight. A penial papilla is present, but seems to be the evaginable part of the deferent duct. The vaginal duct is straight. No accessory gland was found. The fertilization duct is loosely convoluted near the bursa copulatrix. The size of the bursa copulatrix is approximately the same as the size of the receptaculum seminis. Both pouches are spherical-ovate, with a smooth surface.

DIAGNOSTIC FEATURE.— The diagnostic feature of this still unnamed taxon is the color of its dorsal notum.

INFRA-SPECIFIC VARIATION.— Infra-specific variation cannot be evaluated at this stage because only one specimen was fully dissected (the radula of one of the specimens dissected was missing).

DISCUSSION.— These two specimens are part of a new, unnamed species. do not think that

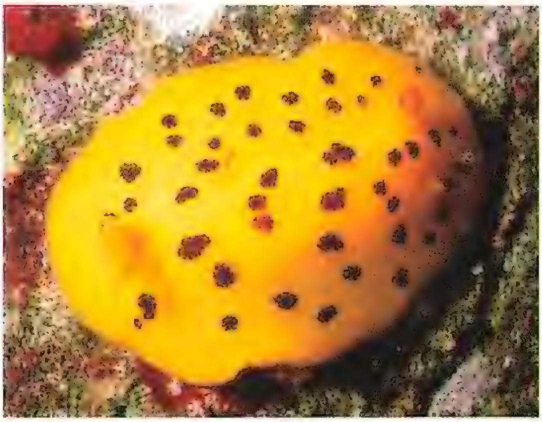

FIGURE 223. *Hiatodoris* sp. B, dorsal color, CASIZ 097537 (R.J. Van Syoc).

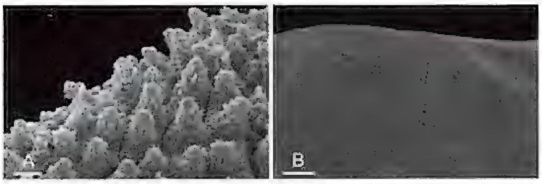

FIGURE 224. *Hiatodoris* sp. B, CASIZ 097537. A. Dorsal notum, tubercles, scale = 100 µm.— B. Smooth labial cuticle, scale = 100 µm.

naming this taxon would be appropriate at this stage because nothing is known about character variation. Other taxonomists might have a different approach and think that there is enough information to name this species. Many problems faced during this study were related to the fact that too new many species names were created without enough data. So, the naming of this species can wait a few more years until additional specimens are available.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test shows that it does not belong to *Discodoris* or *Diaulula* (which is not a clade anyway): it belongs to the new clade *Hiatodoris*, so sp. B should be referred to as *Hiatodoris* sp. B.

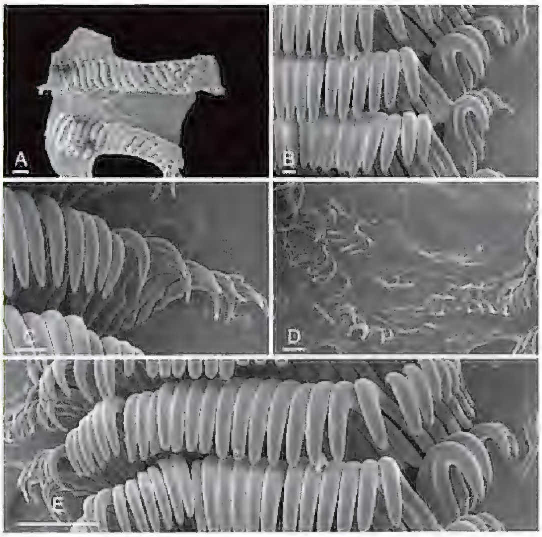

FIGURE 225. *Hiatodoris* sp. B, radula, CASIZ 097537. A. Scale = 200 µm.— B. Outermost teeth, scale = 20 µm.— C. Innermost teeth, scale = 30 µm.— D. Innermost teeth, scale = 30 µm.— E. Right rows, scale = 100 µm.

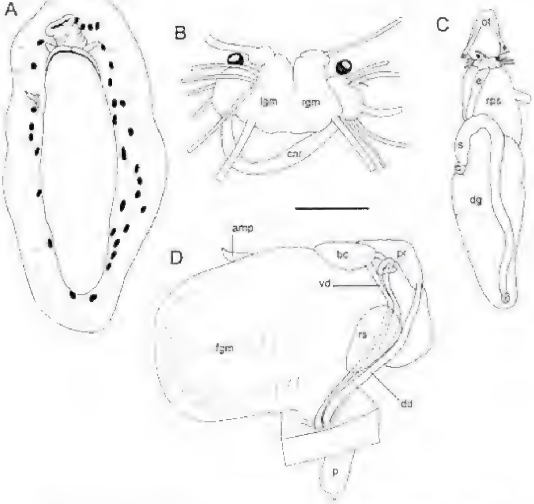

FIGURE 226. *Hiatodoris* sp. B, CASIZ 097537. A. Ventral view, total width = 10 mm.— B. Nervous system, scale = 0.7 mm.— C. General anatomy, scale = 2 mm.— D. Reproductive system, scale = 1.3 mm.

"*Montereina*"

The genus name "*Montereina*" does not refer to a clade (which is emphasized by quotation marks) and thus cannot be characterized by a diagnostic feature, and, also, cannot be defined phylogenetically under the *ICPN*. It refers to a metaphyletic group of species at the base of *Discodorididae*.

Many species (e.g., *Discodoris achroma*, *Discodoris labifera*, *Discodoris rubra*, *Peltodoris lancei*, *Peltodoris lippa*) are transferred from *Discodoris* and *Peltodoris* to another genus because *Discodoris* and *Peltodoris* are restricted to clades to which those species do not belong. Thus, a new genus name is needed under the *ICZN*. Several type species are found in the metaphyletic group at the base of discodorids: *nobilis*, type species of *Montereina* MacFarland, 1905, and *sandiegensis* Bergh, 1878, type species of *Diaulula*, and *zibethina*, type species of *Fracassa*. *Montereina* was selected, despite the fact that it is not the oldest name because: 1) some authors (e.g., Valdés and Gosliner, 2001) use *Diaulula* as a valid genus name of caryophyllidia-bearing dorids; 2) *Fracassa zibethina* clearly is a *nomen dubium*.

"*Montereina*" possesses all the synapomorphies of *Discodorididae*, which are plesiomorphic at its level and thus are not diagnostic of "*Montereina*" only: notched upper lip of the bilabiate anterior foot; digitiform oral tentacles; flattened prostate divided in two (proximal and distal) parts; and two blood glands.

Under the *ICZN*, species binomials may be proposed by using "*Montereina*" for all species that need to be transferred to that genus name: e.g., "*Montereina*" *achroma* (Valdés, 2001), "*Montereina*" *labifera* (Abraham, 1877), "*Montereina*" *rubra* (Bergh, 1905), and "*Montereina*" *lippa* (Valdés, 2001). However, because "*Montereina*" does not refer to a clade, under the *ICPN*, people could also use the combination of *Discodorididae* (the least inclusive clade to which those species belong) with the specific name: e.g., *Discodorididae achroma* (Valdés, 2001), *Discodorididae labifera* (Abraham, 1877), *Discodorididae rubra* (Bergh, 1905), and *Discodorididae lippa* (Valdés, 2001).

Having to transfer quite a few species to *Montereina* is regrettable, but it is a solution that is needed because of the too restrictive nomenclatural rules of the *ICZN* that require that the first parts of binomials are generic names. In that regard, the use of *Discodorididae* instead, allowed under the *ICPN*, will likely provide more stable names, at least for a while (until the phylogeny at the base of discodorids is resolved).

"*Montereina*" *achroma* (Valdés, 2001) new combination
***Discodorididae achroma* (Valdés, 2001) new combination**

Figure 227.

Discodoris achroma Valdés, 2001:274-277, figs 2H, 27-28.

Type material.— Holotype (MNHN, no catalogue number), by original designation: one specimen 12/7 mm preserved, leg. Bertrand Richer de Forges [Musorstom 4 expedition], 3 October 1985. Three paratypes: CASIZ 121098, one specimen 12/7 mm preserved, leg. Philippe Bouchet, Bernard Métivier, and Bertrand Richer de Forges [Biocal expedition], 9 September 1985; MNHN [no registration number], one specimen 12/8 mm preserved, leg. Bertrand Richer de Forges [Musorstom 4 expedition], 3 October 1985; MNHN [no registration number], one specimen 13/9 mm preserved, leg. Philippe Bouchet, Anders Warén, and Bertrand Richer de Forges [Bathus 3 expedition], 30 November 1993.

Type locality.— Off New Caledonia, 22°07′S, 167°11′E, 415-435 meters depth, station CC 245 of the Musorstom 4 expedition. The paratypes also were collected off New Caledonia: 22°11′S, 167°16′E, 495-515 meters depth, station CP 109 of the Biocal expedition; 22°06′S, 167°10′E, 500-550 meters depth, station CP 242 of the Musorstom 4 expedition; Norfolk Ridge, 23°03′S, 166°54′E, 650-659 meters depth, station CP 832 of the Bathus 3 expedition.

Type material condition.— The external condition of the holotype, not dissected by Valdés, is poor: no tubercles could be observed on the smooth and transparent notum; the number of gills could not be determined; the anterior part of the foot is destroyed and the presence of oral tentacles could not be checked. Valdés dissected the two paratypes held by the MNHN. The notum of the paratype collected during the Musorstom 4 expedition is poorly preserved, and no tubercles could be observed; the number of gills could not be determined; the buccal mass and the nervous system are missing; no SEM stubs could be found at the MNHN for the radula and the labial cuticle; the intestine and the digestive gland are still present in the jar; the reproductive system, also present in the jar, was largely destroyed prior to the present study, and is no longer informative. The notum of the paratype collected during the Bathus 3 expedition bears some tubercles, in globally poor shape though; the bucall mass is missing, and no SEM stubs were deposited for the radula and the labial cuticle; the rest of the digestive system and the nervous system are still present; the reproductive system, also present, was largely destroyed and is no longer informative. Finally, the paratype held by the CAS was also dissected by Valdés: the notum, poorly preserved, bears some tubercles; only part of the digestive system (oral tube, digestive gland, stomach, intestine) and the body wall are present in the jar; the reproductive system is missing and the SEM stubs prepared for the radula and the labial cuticle were not deposited at the CAS.

Distribution.— Off New Caledonia, from 415 to 660 meters depth (types). In addition, *achroma* was recorded from the Coral Sea, based on a single, non-type specimen collected at 970 meters during the Musorstom 5 expedition (this specimen, held by the MNHN, was not examined for the present study).

Remarks on the original description (Fig. 227).— The oral tentacles are more or less conical, but not grooved. Radular and labial characters not observable on SEM pictures could not be checked (SEM stubs were not deposited). Also, no feature could be verified concerning the reproductive system, which is missing or destroyed. According to Valdés (2001: fig. 28B), only one duct connects to the bursa copulatrix (the vaginal duct), instead of two ducts (the vaginal duct *and* the fertilization duct); both the fertilization duct (i.e., Valdés's uterine duct) and the duct of the receptaculum seminis originate from the same location along the vaginal duct, creating an organization colloquially called 'in X.' Valdés mentioned an "unarmed penis." Is it unclear whether it is a distinct, permanent penis or just the evaginable distal part of the deferent duct. The actual shape of the penis, a potentially good taxonomic character, was not illustrated by a drawing or a SEM picture. Finally, the nervous system illustrated by Valdés (2001: fig. 28D) is a somewhat stylized representation of the reality (MNHN, Bathus 3): fewer nerves originate from the ganglia.

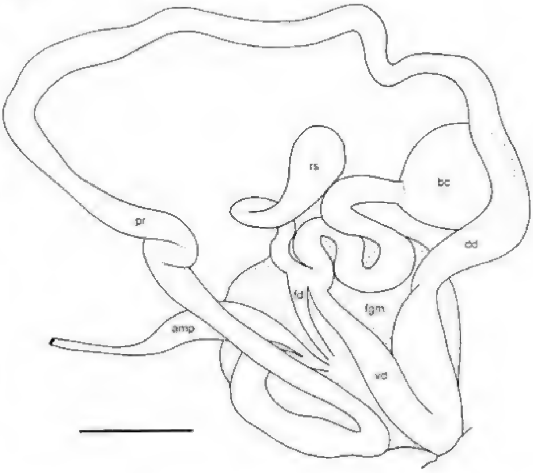

Figure 227. *Discodorididae achroma*, reproductive system, paratype MNHN (Bathus 3), after Valdés (2001: fig. 28B), scale = 1 mm.

Discussion.— Re-examination of the type material was less fruitful than expected because Valdés did not deposit his SEM stubs and the reproductive system was destroyed or missing. Discussing *achroma* is thus limited. The reproductive system 'in X' of *achroma* is an exception in discodoridids. An organization 'in X' is found in chromodorids and dorids (e.g., Rudman 1984), but not in discodorids. Valdés (2001:271) described a similar reproductive system in another, unnamed specimen of *Discodoris*, collected off New Caledonia, at 600 meters depth as well. Valdés argues that this specimen *Discodoris* sp. differs from *Discodoris achroma*. However, all the differences that he mentions (e.g., shape of the radular teeth, size of the vaginal duct, length of the ampulla, etc.) could be due to infra-specific variation, especially because the *achroma* specimens are significantly smaller than the unnamed specimen (I observed such differences in all the species for which I dissected more than just a few specimens). More importantly, Valdés overlooked the fact that he described exactly the same kind of unusual pattern for the reproductive system both in *Discodoris* sp. and *achroma*, and that this pattern was never described in any other species allocated to *Discodoris*. Therefore, either this peculiar pattern is a diagnostic feature of one species from deep waters off New Caledonia, or a feature shared by several closely related species. I think that, at this stage, the first hypothesis should be favored. The presence of a tubular prostate has been observed in a few other discodoridids such as *Paradoris dubia* (Bergh, 1904), but the vast majority of discodorids has a flattened prostate. Interestingly, chromodorids and dorids with a reproductive system 'in X,' also have a tubular prostate, which suggests that these two features could be linked in development.

Supra-specific relationships.— Contrary to what Valdés asserted, *achroma* does not "clearly" belong to *Discodoris*. First of all, *achroma* has a peculiar reproductive system that actually differs from other *Discodoris* species (it is likely that the typical discodorid genital pattern was secondarily modified in *achroma*). Valdés's diagnosis of *Discodoris*, which was not based on phylogenetics, only included plesiomorphies at the level of *Discodorididae* or higher taxa (see Introduction): a phylogenetic test of the relationships of *achroma* shows that it does not belong to the clade *Discodoris*, but instead is part of a metaphyletic group at the base of *Discodorididae*. The Linnaean binomial for *achroma* should be "*Montereina*" *achroma*. Possible names under *ICPN* are "*Montereina*" *achroma* or simply *Discodorididae achroma*.

"*Montereina*" *alba* (White, 1952) new combination
Discodorididae alba (White, 1952) new combination

Figure 228.

Discodoris alba White, 1952:113, fig. 12, plate 6, fig. 5.

Type material.— Holotype (NHM 1934.9.11.105), by monotypy: one specimen 32/15 mm preserved, leg. G. Tandy and J. S. Colman, [no collecting date].

Type locality.— Dry Tortugas, [Caribbean Sea].

Type material condition.— The holotype was dissected by White. The radula and the labial cuticle are missing. No slides could not be found. The reproductive system is still present within the body cavity, but largely uninformative: the different parts (i.e., prostate, female gland mass, spermatic pouches, etc.) cannot be identified.

Distribution.— The holotype is the only specimen known.

Remarks on the original description (Fig. 228).— According to White, the live animal was white. Preserved, it is creamish. White asserted that the spicules were not present in the notum, but some spicules can be observed by transparency, although years of preservation have dissolved most spicules. The "small papillae" described by White do not seem to be caryophyllidia. The oral tentacles are digitiform and not grooved. White's description of the radula could apply to many discodoridid species. The distal part of the reproductive system is missing: the "unarmed penis" that White described is probably lost, which is unfortunate given the importance of penial morphology.

Discussion.— Except for the white color of the live animal, the original description is not helpful and does not allow us to know what *alba* could refer to. White mentioned that the mantle of *alba* contained numerous "small black spots." She probably referred to minute dots that are *with-*

in the mantle and that can be seen with a dissecting miscroscope (at high magnification). The presence of those pigments is confusing and suggest that, maybe, the live animal was not completely white. In fact, Marcus and Marcus (1967a:80) understood from White's description that the dorsal notum of *alba* was bearing some black spots (they do not seem to have examined the type material). In summary, *alba* is regarded as a *nomen dubium*.

Supra-specific relationships.— The classification of *alba* in *Discodoris* was arbitrary: a phylogenetic test of the relationships of *alba* shows that it does not belong to the clade *Discodoris*, but instead is part of a metaphyletic group at the base of *Discodorididae*. The Linnaean binomial for *alba* should be "*Montereina*" *alba*: *Discodoris alba* is phylogenetically inaccurate because *alba* does not belong to the clade *Discodoris*. Possible names under *ICPN* are "*Montereina*" *alba* or simply *Discodorididae alba*.

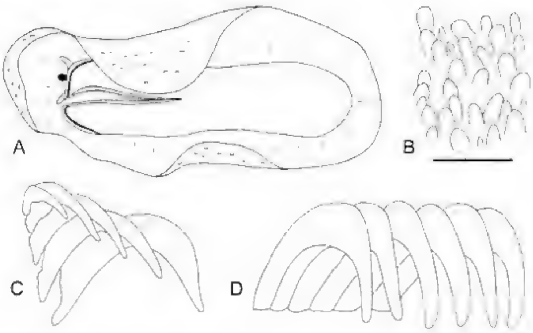

Figure 228. *Discodorididae alba*, holotype. A. Ventral view (as currently preserved), TL = 32 mm.— B. Dorsal notum, tubercles, scale = 0.5 mm.— C. Outermost teeth, after White (1952: fig. 12C).— D. Median teeth, after White (1952: fig. 12B).

"*Montereina*" *aliciae* (Dayrat, 2005) new combination
Discodorididae aliciae Dayrat, 2005

Discodorididae aliciae Dayrat, 2005:216-232, figs 1-5.
Discodoris aliciae.— Behrens and Hermosillo, 2005:70, fig. 129.

Discussion.— The binomial *Discodoris aliciae* is problematic because *Discodoris* refers now to a well-defined clade to which *aliciae* does not belong.

"*Montereina*" *amboinensis* (Bergh, 1890) new combination
Discodorididae amboinensis (Bergh, 1890) new combination
Figure 229.

Discodoris amboinensis Bergh, 1890:895-897, plate LXXXVII, figs 23-27.— Bergh, 1904:48-50, plate III, figs 24-28.— Eliot, 1908:111.

Type material.— Holotype, by monotypy. The holotype could not be found. It is probably lost.

Type locality.— Ambon, Seram, Indonesia.

Distribution.— Bergh (1904) described an additional specimen of *amboinensis* from Roratonga (i.e., Rarotonga), Cook Islands, Pacific Ocean. Eliot (1908) identified an immature specimen from the Red Sea as "perhaps" *amboinensis*. O'Donoghue (1929) just mentioned the possible presence of *amboinensis* in the Red Sea based on Eliot's (1908) contribution.

Occurence.— So far, only three specimens have been identified as *amboinensis*.

Remarks on the original description (Fig. 229).— The preserved animal measured 50/30 mm. Its dorsal notum was yellowish, with faded black-grey, irregularly round spots and dots; the hyponotum and the foot would also bear a multitude of purple-black-grey spots. Bergh provided several general features, such as: conical or hemispherical papillae (0.3 mm diameter) on the dorsal notum, six branchial plumes, 40 rhinophoral lamellae, digitiform oral tentacles, two sickle-shaped jaws. The radular formula is 40 × (68-0-68); however, Bergh mentioned that the edge of the hook of some lateral teeth was finely sculpted in an unusual, characteristic way. Bergh mentioned a 45 mm long intestine, which is quite long for a 50 mm long specimen. However, Bergh did not mention whether this long intestine was straight or coiled, as in *Sebadoris fragilis* (see this species). Bergh's description of the reproductive system, not accompanied by any drawing, is hardly informative: it is unclear whether the prostate is flattened or tubular (although Bergh admitted the presence of a large, flattened prostate as a diagnostic feature of the genus *Discodoris*); the size of the whitish, spherical (4 mm diameter) bursa copulatrix approximately equals the size of the grayish, pear-shaped (4 mm length) receptaculum seminis. The copulatory organ is a conical, 2 mm long penis.

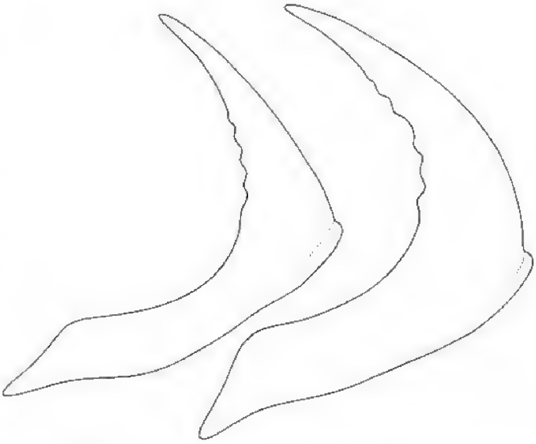

FIGURE 229. *Discodorididae amboinensis*, radular teeth, after Bergh (1890: plate LXXXVII, fig. 26).

DISCUSSION.— In the original description, Bergh only provided one potentially diagnostic feature for *amboinensis*: the wrinkled edge of the lateral tooth hooks. However, Bergh did not find this feature in the second specimen of *amboinensis* that he described from Rarotonga —radular formula 29 × (55-0-55), which suggests that: 1) this second specimen is not part of *amboinensis*; or 2) this feature varies infraspecifically. Eliot (1908) did not mention this feature when he identified an immature specimen from the Red Sea as "perhaps" *amboinensis*— radular formula 26 × (40-0-40). The "yellowish brown [dorsal notum] with darker mottlings" of Eliot's specimen is compatible with many discodorid species, such as *Sebadoris fragilis*, *Discodorididae coerulescens*, and *Peltodoris murrea*. Eliot's description of a "crenulated" branchial pocket is unclear because it does not specifically refer to a five-lobed branchial sheath, as in *Platydoris*. Actually, the edge of the tooth hooks described by Bergh in the holotype may not be diagnostic of any species: it may have been simply been an artifact. The long intestine (considering the size of the holotype) and the presence of a conical penis indicate that *amboinensis* might just be another synonym of *Sebadoris fragilis*, although the latter usually has a bursa copulatrix that is larger than the receptaculum seminis. It seems that *amboinensis* refers to a discodorid, but this species name is regarded as a *nomen dubium* because it is difficult to re-identify specimens as *amboinensis* based on the original description.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *amboinensis* shows that it does not belong to the clade *Discodoris*, but instead is part of a metaphyletic group at the base of *Discodorididae*. The Linnaean binomial for *amboinensis* should be "*Montereina*" *amboinensis*: *Discodoris amboinensis* is phylogenetically inaccurate because *amboinensis* does not belong to the clade *Discodoris*. Possible names under *ICPN* are "*Montereina*" *amboinensis* or simply *Discodorididae amboinensis*.

"*Montereina*" *aurea* (Eliot, 1903) new combination
Discodorididae aurea (Eliot, 1903) new combination

Peltodoris aurea Eliot, 1903:366-367.
Peltodoris cf. *aurea*.— Orr, 1981:44, unnumbered figure.

TYPE MATERIAL.— The three syntypes could not be found.

TYPE LOCALITY.— Wasin [i.e., Wasin Island, off Kenya, western Indian Ocean].

Distribution.— So far, the three syntypes are the only specimen known. Orr's identification of *aurea* specimens from Hong Kong is uncertain.

Remarks on the original description.— Eliot's description of *aurea* is brief and based on three specimens (although Eliot only refers to one specimen throughout the description. The color of live specimens is described thoroughly: "The general color is a rich light orange, due to the back being covered with little flat orange warts on a sandy ground. At regular intervals round the mantle-edge are spots of dull violet; there is also a spot just in front of the gills and one behind the rhinophores. The under side is yellowish with a few brown spots." The maximum length was 22 mm, probably alive, for a 14 mm width. The living animal was flat. According to Eliot, the dorsal notum is not minutely granulated, but "covered with small warts." However, it is difficult to know what Eliot really means by 'warts,' e.g., whether or not they are conical tubercles. There are eight tripinnate gills that "fall in two bundles, right and left" because the gill pocket is contracted in the middle. Interestingly, Eliot describes two tentacles "small and button-like" as well as a grooved anterior foot with a notched superior lip. There is no labial armature. The tentacles are thin and digitate. The labial cuticle is smooth; the radular formula is 20 × (25-0-25); all teeth are simply hamate —the innermost and outermost teeth are smaller, but "not conspicuously." The stomach is free. Eliot also indicates that he did not find any armature in the reproductive system.

Discussion.— Eliot did not compare *aurea* to any existing species, even within *Peltodoris* in which he placed this species because of "the stiffness and small radula." Actually, Eliot admitted that he had "some hesitation in classifying this specimen as *Peltodoris*, as the back is not minutely granulated but covered with small warts." However, Eliot did not wish to describe this species as a new *Archidoris* because, according to him, this genus had a different shape. The presence of a notched superior lip of the anterior foot indicates that *aurea* should belong to *Discodorididae*. The presence of button-like tentacles (instead of digitiform tentacles) is confusing, but such tentacles have been described in other discodorid species, such as *Thordisa diuda* Marcus, 1955 (the latter also has digitiform tentacles, in addition to oral pits; see, Chan and Gosliner, 2007). However, *aurea* is not regarded as a *nomen dubium* because the description of the color of the live animals should allow people to re-identify it. However, there is no reason to classify *aurea* within *Peltodoris*. Narayanan (1971) identified a specimen from the Gulf of Kutch as *Peltodoris rubescens* Bergh, 1905, and briefly compared it with *aurea*. Finally, Orr (1981) published a picture of a specimen he tentatively identified as *Peltodoris* cf. *aurea*, but the dorsal color of the animal (creamish-yellowish) does not fit with Eliot's original description.

Supra-specific relationships.— A phylogenetic test of the relationships of *aurea* shows that it does not belong to the clade *Peltodoris*, but instead is part of a metaphyletic group at the base of *Discodorididae*. The Linnaean binomial for *aurea* should be "*Montereina*" *aurea*: *Peltodoris aurea* is phylogenetically inaccurate because *aurea* does not belong to the clade *Peltodoris*. Possible names under *ICPN* are "*Montereina*" *aurea* or simply *Discodorididae aurea*.

"*Montereina*" *aurila* (Marcus and Marcus, 1967) new combination
Discodorididae aurila (Marcus and Marcus, 1967) new combination

Figures 230-240.

Discodoris aurila Marcus and Marcus, 1967a:85-87, figs 108-111.— Keen, 1971:823-825.
Diaulula aurila.— Camacho-García and Valdés, 2003:75-78, fig. 1D, figs 6-7.— Berhens, 2004:41.
Discodoris sp. 1 Behrens, 1991:67, fig. 117.— Goddard and Schickel, 2000:21.— Berhens, 2004:41.

Type material.— Two syntypes (NMNH 576268, slides F-814 and F-815): two specimens 20/10 (#1) and 15/12 (#2) [the posterior part is missing; the specimen was probably longer], leg. F. Bayer, December 1962.

Type locality.— Deale Beach, Pt. Kebbe Beach, Pacific side of the Panama Channel, [Pacific Ocean].

Type material condition.— One syntype (#2) was fully dissected by Eveline and Ernst Marcus: the radula, the labial cuticle, and the reproductive system are preserved on two slides (F-814 and F-815). One piece of the notum of this specimen was prepared for SEM in the present study. The other syntype (#1) was still complete. It was opened to verify whether or not the labial cuticle is armed with jaws. The notum of both specimens is poorly preserved. In particular, the spicules have been dissolved due to fixation and preservation.

Additional material dissected.— **Costa Rica**, Pacific Coast, Puntarenas Province, Cabo Blanco, San Miguel Station, 26 January 1999, one specimen 9/5 mm preserved, leg. F. Alvarando, identified as *Discodoris aurila* by Yolanda Camacho-Garcia (CASIZ 159788); **Mexico**, Baja California Sur, Pacific Ocean, Bahia Tortugas, (below centro de Aquacultura), 29 June 1984, one specimen 27/17 mm preserved, leg. Hans Bertsch, identified as *Discodoris* by Hans Bertsch (CASIZ 072900); Mexico, Baja California Sur, Pacific Ocean, Bahia Tortugas, (below centro de Aquacultura), 1 July 1984, five specimens 28/22 (#1), 28/18 (#2), 25/16 (#3), 25/16 (#4), and 24/14 (#5) mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 072898) [the specimens #4 and #5 were opened ventrally before the present study; the buccal mass was missing in both specimens]; Mexico, Baja California Sur, Pacific Ocean, Bahia Sebastian Vizcaino, 16 miles East of Punta Falsa, 1 mile East of small lighthouse near Campositas, 3 meters depth, 30 June 1984, one specimen 17/10 mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 072897); Mexico, Baja California Norte, Pacific Coast, Punta Rosarito, 28°33.75′N, 114°09.30′W, 29 March 2000, four specimens 12/7 (#1), 8/6 (#2), 8/6 (#3), 7/5 (#4) mm preserved, leg. J. H. R. Goddard and E. Schickel Goddard, identified as *Discodoris* by J. H. R. Goddard and E. Schickel Goddard (CASIZ 122177) [voucher specimens: Goddard and Schickel (2000) suggested that these specimens belong to *Discodoris* sp.1 Berhens, 1991].

Distribution.— Panama (type locality), Costa Rica (Camacho-García and Valdés, 2003; present study), Pacific coasts of Baja California (Berhens, 1991; Goddard and Schickel, 2000; both as *Discodoris* sp.1; present study). The current northernmost locality is Punta Rosarito (28°33.75'N).

Occurence.— This species is well represented in collections from the Pacific coasts of both Costa-Rica and Mexico. Its more rare occurrence from the Pacific coasts of Panama might simply be the result of fewer collecting trips.

Habitat.— Goddard and Schickel (2000:21) found *aurila* (as Berhens's *Discodoris* sp. 1) in two intertidal sites "part of a larger, continuous cobble field, with at our second site grades into low rock shelf pocketed with small tidepools." Rocky intertidal (CASIZ 072900).

Literature.— Several publications provide information about the color of live animals and the external morphology (Marcus and Marcus, 1967a; Berhens, 1991, as *Discodoris* sp. 1; Goddard and Schickel, 2000, as Berhens' *Discodoris* sp. 1; Camacho-García and Valdés, 2003, as *Diaulula aurila*). Marcus and Marcus (1967a) and Camacho-Garcia and Valdés (2003) provided some anatomical data. Eveline and Ernst Marcus did not provide any information about character variation because they dissected only one specimen. Although they have examined many specimens, Camacho-García and Valdés provided almost no information about character variation either. Finally, Keen (1971) simply summarized the original description without adding new data.

Remarks on the original description (Figs. 231-232).— The original description of *aurila* by Eveline and Ernst Marcus is problematic. First of all, the caryophyllidia they mentioned could not be observed in the syntypes because of the poor preservation of the notum. SEM pictures did not solve this issue: indeed, the 'spicule-free' tubercles found are difficult to interpret; they could be caryophyllidia but it is quite uncertain. The second problem concerns the labial cuticle. According to Eveline and Ernst Marcus, the labial cuticle is armed with jaws. However, their drawing is not really convincing. Also, the labial cuticle they mounted is not well prepared: it is not flat, and the actual surface of the labial cuticle cannot be seen; it seems that the labial cuticle they prepared does not present jaws in the strict sense. However, some structures on the edge of the labial cuticle could be interpreted as rodlet tips. The second syntype, opened for the present study, has clearly neither jaws nor any rodlets on the labial cuticle: thus, the drawing by Eveline and Ernst Marcus was first interpreted as some muscles on the surface of the labial cuticle instead of real rodlets. However, a few non-type specimens were found with a clearly smooth labial cuticle bearing just a few rodlets on each lateral side of the labial cuticle. Therefore, it is very likely that the labial cuticle prepared by the Marcus is smooth, but bear some isolated rodlets. This feature is exceptional. In fact, *aurila* is the only species found within this study with a smooth labial cuticle with a few isolated rodlets but no real jaws. The organization of the reproductive system (without taking it out from the body wall) was also checked: it clearly is similar to the reproductive system of the other specimens described here; in particular, it presents the loop of the fertilization duct on top of the receptaculum seminis, which is a good diagnostic feature. The deferent duct of the reproductive system illustrated by the Marcus is almost straight. This, however, might be due to the fact that the reproductive system that they drew was preserved on a slide. In the other syntype, the deferent duct presents several loops. Also, the surface of the receptaculum seminis of the reproductive system prepared by the Marcus is smooth, as they illustrated. However, the surface of the receptaculum seminis of the other syntype is granulated. In both syntypes, the bursa copulatrix is much larger than the receptaculum seminis. Finally, the slide of the reproductive system prepared by the Marcus shows that the disappearance of the fertilization duct into the female gland mass is not marked by a duct. Several radular features were verified: the radular formula —23 × (45-0-45)— is basically the same as the formula described by the Marcus —24 × (47-0-47)— because some teeth and rows are difficult to observe. All teeth are simply hamate, including the outermost ones. They bear no denticles. Finally, both syntypes are whitish, but also bear some black dots on the dorsal surface. The grey line illustrated by Eveline and Ernst Marcus is still present in one specimen but largely faded in the other, probably due to preservation.

Description of new specimens (Figs. 230, 233-240).— *Color*: The ground color of the dorsal notum of live animals varies from orange (e.g., CASIZ 072900) to brown (e.g., CASIZ 072898, CASIZ 072897), and bears both white and dark brown speckles. The latter are more or less randomly located on the notum, although they may be more concentrated along the median line; their abundance varies too. Preserved specimens are yellowish or white; black dots sometimes are preserved (e.g., CASIZ 122177, CASIZ 159788). The ground color of the ventral surface (hyponotum and foot) is similar to the color of the dorsal notum.

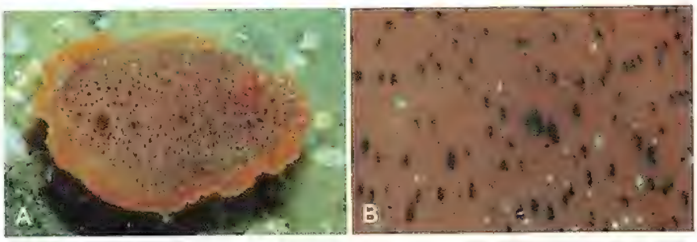

Figure 230. *Discodorididae aurila*, dorsal color. A. CASIZ 072898 (one of five specimens, T.M. Gosliner).— B. Same as A, detail.

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The width of the foot equals approximately one half of the width of the dorsal notum (in preserved specimens). The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform and not grooved. The dorsal notum bears tubercles that are caryophillidia, for the most part. However, some tubercles were found that are obviously not caryophyllidia, with spicules protruding not in a regular circle but rather in a disorganized manner upon the entire surface of the tubercle (e.g., 072898 #4). The apex of the tubercles seems to be always ciliated. Small holes (diameter < 10 µm) and many small tufts of cilia were found on the mantle, including the gills and the rhinophores. In preserved specimens, the margins of the rhinophoral and branchial sheaths can be smooth or lightly crenulate. There are six tripinnate branchial plumes arranged in circle around the anus; specimens with seven branchial plumes were found (CASIZ 072898). The rhinophores have from thirteen to twenty lamellae, depending on the size of the animals.

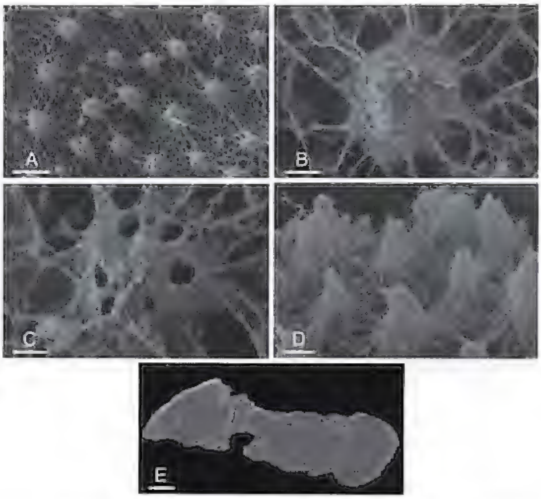

FIGURE 231. *Discodorididae aurila*, syntypes (NMNH 576268). A. Dorsal notum, syntype #2, scale = 100 µm.— B. Dorsal notum, tubercle, syntype #2, scale = 20 µm.— C. Dorsal notum, tubercle, syntype #2, scale = 20 µm.— D. Dorsal notum, syntype #2, scale = 40 µm.— E. Smooth labial cuticle, syntype #1, scale = 200 µm.

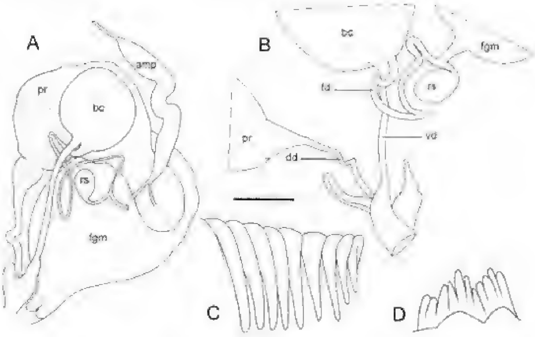

FIGURE 232. *Discodorididae aurila*. A. Reproductive system, syntype (#2), after Marcus and Marcus (1967a: fig. 111).— B. Reproductive system, syntype (#2), slide F-815, scale = 1 mm.— C. Outermost teeth, syntype (#2), slide F-814, scale = 65 µm.— D. Isolated jaw rodlets, syntype (#2), slide F-814, scale = 50 µm.

Digestive system. The stomach is large, free on top of the anterior side of the digestive gland. A caecum is present. The intestine is straight and dorsal. The labial cuticle is unarmed. With the dissecting microscope, it was impossible to see any rodlets. Indeed, no specimens had a pair of fully developed lateral jaw plates. However, the labial cuticle of several individuals (CASIZ 072898 #2 and #4, CASIZ 122177 #3 and #4) bears a few rodlets on both lateral sides. These rodlets are undistinguishable without SEM. The other labial cuticles seem to be entirely smooth. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. The radular formulae are: 13 × (20-0-20) in a 7 mm long specimen (CASIZ 122177 #4), 12 × (20-0-20) in a 8 mm long specimen (CASIZ 122177 #2), 13 × (20-0-20) in a 8 mm long specimen (CASIZ 122177 #3), 16 × (29-0-29) in a 12 mm long specimen (CASIZ 122177 #1), 13 × (30-0-30) in a 9 mm long specimen (CASIZ 159788), 16 × (34-0-34) in a 17 mm long specimen (CASIZ 072897), 17 × (38-0-38) in a 17 mm long specimen (CASIZ 072897), 22 × (34-0-34) in a 25 mm long specimen (CASIZ 072898 #3), 21 × (40-0-40) in a 27 mm long specimen (CASIZ 072900), 17 × (40-0-40) in a 28 mm long specimen (CASIZ 072898 #1) although some rows were lost during the preparation, and 24 × (43-0-43) in a 28 mm long specimen (CASIZ 072898 #2). Some rows were missing in one specimen due to the preparation (CASIZ 072898 #1). Rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the five or ten innermost teeth of which the size increases gradually and the last three or four outermost ones of which the size decreases gradually. All teeth are hamate, although the last two outermost ones can be straight (because of their reduced size). All teeth are not grooved. They bear

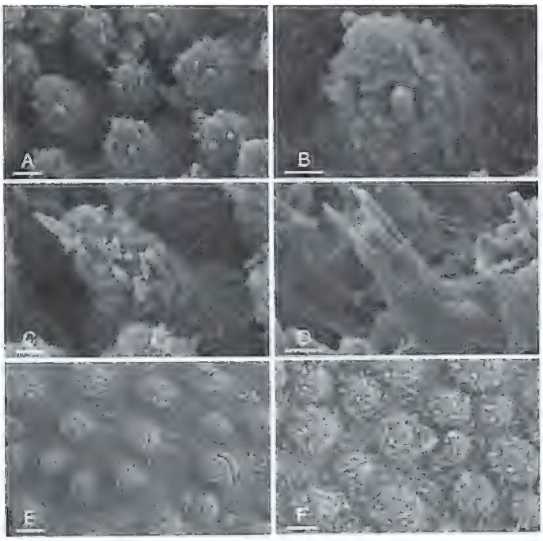

FIGURE 233. *Discodorididae aurila*, dorsal notum, tubercles. A. CASIZ 072898 (#3), scale = 60 µm.— B. CASIZ 072898 (#3), scale = 30 µm.— C. Tubercle, CASIZ 072898 (#4), scale = 30 µm.— D. CASIZ 122177 (#4), scale = 20 µm.— E. CASIZ 072900, scale = 100 µm.— F. CASIZ 072897, scale = 60 µm.

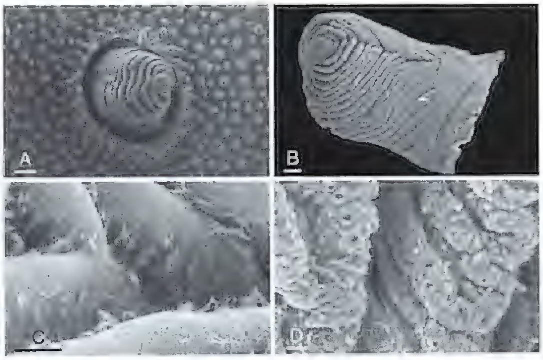

FIGURE 234. *Discodorididae aurila*. A. Rhinophore, CASIZ 072898 (#3), scale = 200 µm.— B. Rhinophore, CASIZ 072898 (#1), scale = 100 µm.— C. Rhinophore, detail, CASIZ 072898 (#1), scale = 20 µm.— D. Branchial plume, detail, CASIZ 072898 (#1), scale = 30 µm.

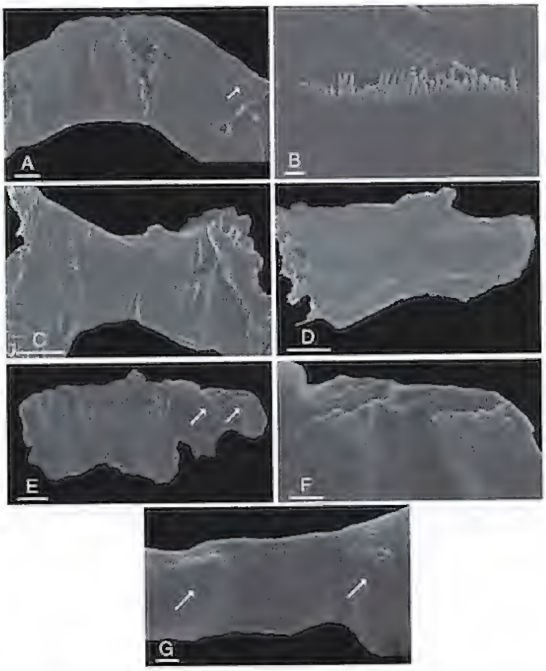

FIGURE 235. *Discodorididae aurila*, labial cuticle. A. Labial cuticle armed with a few isolated rodlets, CASIZ 072898 (#2), scale = 200 µm.— B. Isolated rodlets, CASIZ 072898 (#2), scale = 20 µm.— C. Smooth labial cuticle, CASIZ 072900, scale = 200 µm.— D. Smooth labial cuticle, CASIZ 072897, scale = 200 µm.— E. Labial cuticle armed with a few isolated rodlets, CASIZ 122177 (#4), scale = 100 µm.— F. Isolated rodlets, CASIZ 122177 (#4), scale = 30 µm.— G. Isolated rodlets, CASIZ 122177 (#3), scale = 20 µm.

no denticles except for the outermost ones: from zero to five denticles are present at the apex of the two outermost teeth. However, note that the presence/absence and the number of those denticles vary among the rows of a single radula: the two outermost teeth of CASIZ 072900, and CASIZ 072898 #1 and #2 are smooth; denticles were found in all other specimens. The strongest denticles were found in the specimen from Costa Rica (CASIZ 159798).

Nervous system. The length of the circum-esophageal nerve ring may be equal to the width of the two cerebro-pleural ganglia or may be equal to three times their width. The cerebral and pleural ganglia are fused. The surface of the ganglia is smooth.

Reproductive system. The ampulla is convoluted, with from one to three loops. The division between male and female ducts (hidden within the female gland mass) could not be seen by dissection. The prostate is divided in two parts, a proximal whitish part and a distal yellowish-orange part. The deferent duct is tightly or loosely convoluted, with up to five tight loops (e.g., CASIZ 072897). No distinct penis could be found. The vaginal duct is straight. No accessory gland was found. The fertilization duct is convo-

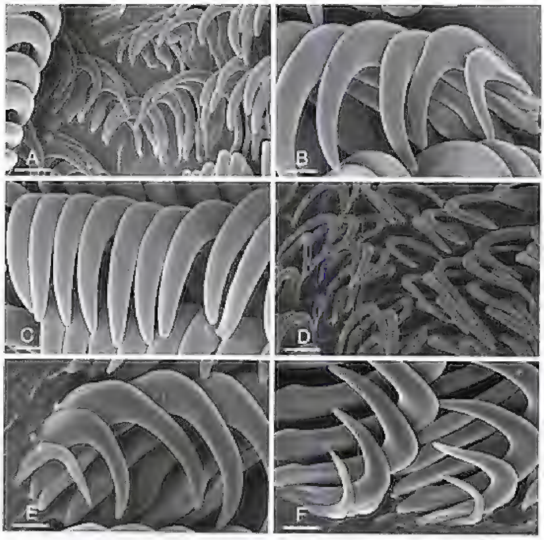

FIGURE 236. *Discodorididae aurila*, radula. A. Innermost teeth, CASIZ 072898 (#1), scale = 40 µm.— B. Outermost teeth, CASIZ 072898 (#1), scale = 20 µm.— C. Median teeth, CASIZ 072898 (#1), scale = 20 µm.— D. Innermost teeth, CASIZ 072898 (#2), scale = 40 µm.— E. Outermost teeth, CASIZ 072898 (#2), scale = 20 µm.— F. Outermost teeth, CASIZ 072898 (#3), scale = 20 µm.

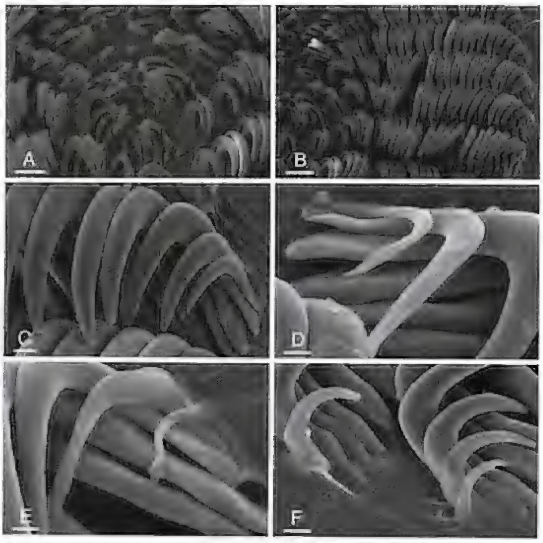

FIGURE 237. *Discodorididae aurila*, radula. A. Innermost teeth, CASIZ 122177 (#1), scale = 40 µm.— B. Right rows, CASIZ 122177 (#1), scale = 60 µm.— C. Outermost teeth, CASIZ 122177 (#1), scale = 10 µm.— D. Outermost teeth, CASIZ 122177 (#2), scale = 5 µm — E. Outermost teeth, CASIZ 122177 (#2), scale = 5 µm.— F. Outermost teeth, CASIZ 122177 (#3), scale = 10 µm.

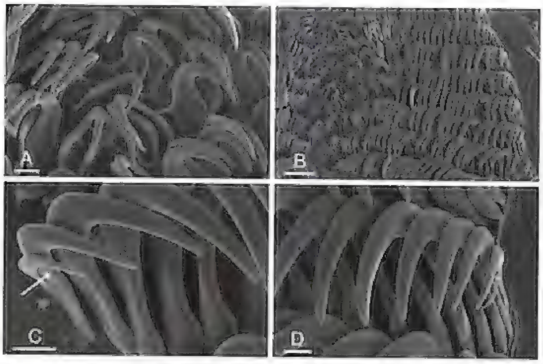

FIGURE 238. *Discodorididae aurila*, radula. A. Innermost teeth, CASIZ 072897, scale = 20 µm.— B. Right rows, CASIZ 072897, scale = 100 µm.— C. Left outermost teeth, CASIZ 072897, scale = 20 µm.— D. Right outermost teeth, CASIZ 072897, scale = 20 µm.

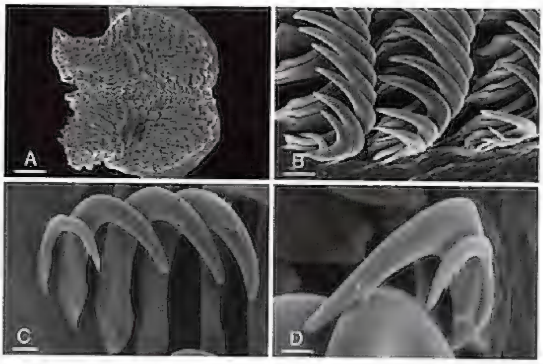

FIGURE 239. *Discodorididae aurila*, radula. A. CASIZ 072900, scale = 300 µm.— B. Right outermost teeth, CASIZ 072900, scale = 30 µm.— C. Left outermost teeth, CASIZ 159798, scale = 10 µm.— D. Right outermost teeth, CASIZ 159798, scale = 5 µm.

luted. Its three to seven —loose or tight— loops are located near the receptaculum seminis, usually on top of it and the female gland mass. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is not marked by a clear duct. It cannot be seen externally because it is hidden by the receptaculum seminis. The bursa copulatrix is much larger than the receptaculum seminis and is largely covered by the prostate. This character could not be verified in the specimen from Costa Rica because the small reproductive system was homogeneously white, and identifying the organs was not possible. The bursa copulatrix is ovate and tends to be quite elongated. The receptaculum seminis can be spherical or ovate; its surface is smooth (e.g., CASIZ 072897) or covered with small rounded protuberances (e.g., CASIZ 072898).

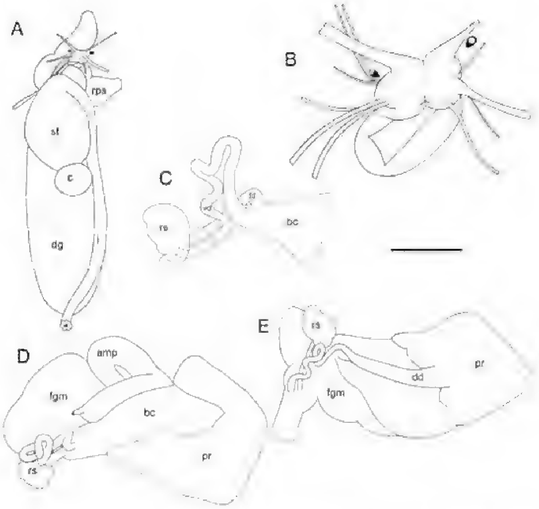

FIGURE 240. *Discodorididae aurila*, CASIZ 072898 (#1). A. General anatomy, scale = 3.5 mm.— B. Nervous system, scale = 1 mm.— C. Reproductive system, spermatic ducts, scale = 1.3 mm.— D. Reproductive system, scale = 1.8 mm.— E. Reproductive system, scale = 1.8 mm.

DIAGNOSTIC FEATURES.— The best diagnostic character of *aurila* certainly is the color of the dorsal notum. Although the ground color may vary (see below), the presence of white and black speckles is a distinct feature. Terry Gosliner used to colloquially describe this feature as a "salt and pepper" pattern. A potentially good diagnostic anatomical character is the general organization of the reproductive system. The latter presents a combination of features that makes it quite distinguishable from other species, such as the large, elongated, bursa copulatrix embedded within the prostate, and the presence of loops of the fertilization duct just on top of the receptaculum seminis. However, these two anatomical characters (useful for identifying preserved specimens with poor or no color information) should be used cautiously because 1) they may be present in specimens that are not part of *aurila* and 2) infra-specific variation within *aurila*.

INFRA-SPECIFIC CHARACTER VARIATION.— The present study and the literature give a good idea of the variation of the ground color of the dorsal notum of live animals: pale gray, yellowish, orange, and brown. Camacho-García and Valdés (2003) do not mention how many labial cuticles they prepared for SEM: a small number of preparations might explain why they did not observe the isolated rodlets found here. The number of radular rows varies from 12 to 24, and the number of teeth per row varies from 20 to 43, depending on the size of the animal. The radular formula from the original description and the formula mentioned by Camacho-García and Valdés (2003) are both compatible with this range of variation. Neither the Marcus nor Camacho-García and Valdés have described the presence of denticles on the outer edge of the hook of the two outermost teeth: this certainly is a consequence of the fact that both descriptions were based on a single radula (the Marcus dissected only one syntype and Camacho-García and Valdés mentioned only one radular formula). Also, note that the radula is symmetrical, not asymmetrical. The correct formula probably was 20 × (30-0-30), not 20 × (39-0-30) for a 15 mm long specimen (as written in Camacho-García and Valdés 2003). Concerning the reproductive system, there is see no reason to consider the ampulla "very long" (Camacho-García and Valdés 2003). Also, the bursa copulatrix is only twice as large as the receptaculum seminis in the reproductive system drawn by Camacho-García and Valdés (2003), and is not covered by the prostate. However, Camacho-García and Valdés illustrated a single reproductive system and did not discuss individual variation. Therefore, it is difficult to determine whether specimens from Costa Rica have a significantly smaller bursa copulatrix or if the relative size of the spermatic pouches varies (as in most species studied here).

DISCUSSION.— The fact that the syntypes of *aurila*, the specimens from Mexico dissected here, and the specimens studied by Camacho-García and Valdés (2003) from Costa-Rica (one Costa-Rican specimen was dissected in the present study too) are part of the same entity is well supported. First, they all share black and white speckles on the dorsal notum, as well as several distinctive anatomical features, especially in the reproductive system. Finally, and more importantly, an interesting feature was observed here for the first time in discodorids: in one of the two syntypes of *aurila* and several specimens from the Mexican coasts (CASIZ 072898), the labial cuticle is not armed with a pair of jaws but instead with a few isolated rodlets on each lateral side of the labial cuticle. This probably explains why Eveline and Ernst Marcus described jaws, although fully developed jaw plates are absent. This observation has broader implications because it shows that the genetic tools involved in the presence/absence of jaws could be turned on and off easily (note that no infra-specific variation for this character has been formerly demonstrated in discodorids), which supports the idea that jaws could have been lost and re-acquired many times during the evolution of *Discodorididae* (which can only be tested by mapping the character on a well-resolved phylogeny).

Supra-specific relationships.— Two supra-specific affinities have been proposed so far for *aurila* (*Discodoris* and *Diaulula*), none of them supported by phylogenetic analyses. A phylogenetic test of the relationships of *aurila* shows that it does not belong to the clade *Discodoris*, but instead is part of a metaphyletic group at the base of *Discodorididae*. Also, no synapomorphies could be identified for *Diaulula* (and nobody else has ever demonstrated that *Diaulula* was a clade): the generic name *Diaulula* has been used for caryophyllidia-bearing dorids that do not positively belong to any other genera of caryophyllidia-bearing dorids. The Linnaean binomial for *aurila* should be "*Montereina*" *aurila*: *Discodoris aurila* and *Diaulula aurila* are both phylogenetically inaccurate because *aurila* does not belong to the clade *Discodoris* and because *Diaulula* is not a clade. Possible names under *ICPN* are "*Montereina*" *aurila* or simply *Discodorididae aurila*.

"*Montereina*" *branneri* (MacFarland, 1909) new combination
Discodorididae branneri (MacFarland, 1909) new combination

Figures 241-257.

Doris (*Dendrodoris*) *crucis* Ørsted *in* Mörch, 1863:33-34 [in part, not *crucis* Ørsted *in* Mörch, 1863].
Discodoris notha Bergh, 1877a:530-532, plate LXI, figs 29-30, plate LXII, figs 3-9.— Bergh, 1884a:92.— Bergh, 1904:53-54, plate IV, figs 7-14. [in part, not *notha* Bergh, 1877].
Discodoris branneri MacFarland, 1909:66-72, plate XII, figs 58-65.— Marcus, 1955:145-146.— Marcus and Marcus, 1967a:78.
Carminodoris branneri.— Perrone and Doneddu, 1997:52.
Discodoris evelinae Marcus, 1955:143-147, figs 141-150.— Marcus and Marcus, 1967a:75.— Marcus and Marcus, 1969:13.— Marcus, 1970:944.— Marcus and Hughes, 1974:520, fig. 41.— Bertsch, 1976:117-122.— Marcus, 1976a:121, 139.— Meyer, 1977:301.— Humann, 1992:241, unnumbered figure.— Redfern, 2001:175, plate 119, fig. 725. **New synonym.**
Discodorididae evelinae.— Dayrat and Gosliner, 2005:205.
Discodoris hedgpethi Marcus and Marcus, 1960b:254-256, figs 7-11.— Marcus and Marcus, 1967a:75-78, figs 98A-E.— Marcus and Marcus, 1970a:62-63, figs 111-114. **New synonym.**
Discodoris spetteda Marcus and Marcus, 1966:181. *Nomen nudum* (Marcus and Marcus, 1967a).

Type material (*crucis*).— One paralectotype (ZMUC no catalogue number, referred to as type specimen #3), designated here: St. Thomas, [Virgin Islands], Vestindien [West Indies], one specimen 53/25 mm preserved, leg. Riise, [no collecting date]. Prior to the present study, the type material of *crucis* would include four syntypes. A lectotype was designated to solve a nomenclatural issue: one syntype (dissected for the present study) was part of *branneri*; one syntype (dissected for the present study) was part of *Tayuva lilacina*; the two other syntypes (dissected by Bergh) could be part of several species — both the original description and Bergh's re-description are vague and largely uninformative (see *crucis*) — although they could hardly be part of *branneri* because of the absence of the strongly armed penis. The fact that a paralectotype of *crucis* is part of *branneri* is no longer an issue because only the lectotype has a name-bearing function (although the paralectotypes are still part of the type material of *crucis*). This paralectotype of *crucis* can be considered as a former syntype that was misidentified as *crucis*, and the name *crucis* is not a synonym of *branneri*.

Type material (*notha*).— Two paralectotypes (ZMUC GAS-2126), designated here: [Caribbean Sea], Guadeloupe, two specimens 45/27 (#1) and 36/27 (#2) mm preserved, leg. Schramm, [first called *D. crucis* by Mørch], [no collecting date]. Prior to the present study, the type material of *notha* would include four syntypes (ZMUC GAS-2126 and 2127). A lectotype (ZMUC GAS-2127 #1) is designated to solve a nomenclatural issue: two syntypes from Guadeloupe were part of *branneri* and their anatomy was not be compatible with the original description that was largely based on the two other syntypes, from St. Thomas, Virgin Islands (see *Discodorididae notha* for more details). The fact that two paralectotypes of *notha* are part of *branneri* is no longer an issue because only the lectotype has a name-bearing function: the two paralectotypes of *notha* can be considered as two former syntypes that were misidentified as *notha*, and *notha* is not a synonym of *branneri*.

Type material (*branneri*).— Holotype (CASIZ 020019), by monotypy: one specimen 29/15 mm preserved, leg. A. W. Greeley, 1899. The CAS also holds a series of slides (#021009) for the internal anatomy (histological slides of the reproductive system, radula, jaws). Note that this type material is the former type material #146 from the Invertebrate Series, Leland Stanford Junior University Zoological Museum.

Type material (*evelinae*).— The two syntypes of *evelinae* could not be found. However, they could be at the MZSP, because part of the Marcus' collection has not been fully curated (pers. com., Dr Luiz Simone).

Type material (*hedgpethi*).— Three syntypes (MZSP 37968): three specimens 40/25 (#1), 36/24 (#2), and 29/13 (#3) [foot sole only, specimen cut in pieces by Marcus] mm preserved, leg. J. W. Hedgpeth, 12 October 1948. The original description was based on three specimens "up to 45 mm long," among which Marcus designated a holotype (45 mm preserved), but no paratypes. The jar with the holotype of *hedgpethi* contains the remaining pieces of three dissected specimens, and the holotype cannot be distinguished from the two additional, non-type specimens. The fact that Marcus mentioned that the preserved holotype was 45 mm implies that specimen #1 may be the holotype. However, the size of the pedal sole of the third specimen (29 mm) could be part of a large specimen as well. Because the holotype cannot be identified with certainty, specimens #1, #2, and #3 should be considered equivalent to syntypes. Besides, Marcus dissected and used them all for the original description of *hedgpethi*. This material, part of the Marcus' collection (#138), was deposited in the Department of Zoology, University of São Paulo, Brazil, and then transferred to the MZSP.

Type locality (*crucis*).— The type locality of *crucis* is the locality of the lectotype. The locality of the paralectotype, St. Thomas, Virgin Islands, is the same as the type locality of *crucis*, but it is not *per se* the type locality.

Type locality (*notha*).— The type locality of *notha* is the locality of the lectotype, St. Thomas, Virgin Islands. The locality of the two paralectotypes considered here, Guadeloupe, is not the type locality of *notha*.

Type locality (*branneri*).— Riacho Doce, Alagoas, northeastern coasts of Brazil.

Type locality (*evelinae*).— Island of São Sebastião, off São Paulo, Brazil.

Type locality (*hedgpethi*).— Port Aransas, Texas, USA.

Type material condition (*crucis*).— The paralectotype dissected for the present study was still complete. See *crucis* for information about the lectotype and the two other paralectotypes, all of which are not part of *branneri*.

TYPE MATERIAL CONDITION (*notha*).— One of the two paralectotypes (ZMUC 2126 #1) was dissected by Bergh. The body wall, the digestive gland, the intestine, the penis and the ampulla remain in the jar. The other paralectotype (ZMUC 2126 #2) was dissected for the present study. For information about the lectotype and the third paralectotype, which are not part of *branneri*, see *notha*.

TYPE MATERIAL CONDITION (*branneri*).— The holotype of *branneri* was entirely dissected by MacFarland. Only the body wall and the digestive gland remain in the jar. The radula, the jaws and the reproductive system are preserved on slides.

TYPE MATERIAL CONDITION (*evelinae*).— Unknown.

TYPE MATERIAL CONDITION (*hedgpethi*).— Marcus dissected the three syntypes for the original description. The notum of the specimen #1 is almost complete: a small piece of the dorsal notum was cut, and the area around the genital opening was cut as well. Its buccal mass and its reproductive system are missing (the specimen was opened ventrally). The notum of the specimen #2 is complete, except for the area cut around the genital opening. Its buccal mass and its reproductive system are missing (the specimen was opened ventrally). The specimen #3 is a pedal sole with a digestive gland attached to it, and a few pieces of notum. In addition, the jar contains several organs that could not be attributed to any particular specimen: an almost complete reproductive system (penial sheath and penis missing), two destroyed pieces of apparently two different reproductive systems (because there are two ampullae); two penises (mounted on SEM stubs for the present study).

ADDITIONAL MATERIAL DISSECTED.— **Florida**, Key Biscayne, [Bear Cut], [21 March 1965], one specimen 56/40 mm preserved length, leg. Bayer, identified by (USNM 576292) [this specimen is the holotype of *spetteda* Marcus and Marcus, 1966, a *nomen nudum* (Marcus and Marcus 1967a); it was described by Marcus and Marcus (1967) under the name *hedgpethi*; the jaws and the radula are preserved on the slide F-854, almost dry; the penis is preserved on the slide F-855]; **Bahamas**, Grand Bahamas Island, 25 miles East of Freeport, Gold Rock Creek, April 1984, two specimens 45/30 (#1) and 38/25 (#2) mm preserved, leg. J. N. Worsfold, identified as *Discodoris* by T. M. Gosliner (CASIZ 072292); **Panama**, Caribbean Sea, Canal Zone, Galeta Island, 29 August 1974, three specimens 45/28 (#1), 43/27 (#2), and 40/20 (#3) mm preserved, leg. Hans Bertsch, identified as *Discodoris evelinae* by H. Bertsch (CASIZ 010570) [specimens dissected by H. Bertsch, only two radula slides #186 (spm #1) and #187 (spm #3) found, slide #185 (spm #2) could not be found; labial cuticles were missing]; Panama, Caribbean Sea, Canal Zone, East of Galeta Island, 1 September 1974, one specimen 27/25 mm preserved, leg. H. Bertsch, identified as *Discodoris evelinae* by H. Bertsch (CASIZ 010571) [specimen dissected by H. Bertsch, radula slide # 195; the labial cuticle was missing]; Panama, Caribbean Sea, Canal Zone, East of Galeta reef flat, 24 August 1974, two specimens 60/35 and 45/25 mm preserved, leg. H. Bertsch, identified as *Discodoris evelinae* by H. Bertsch (CASIZ 010572) [specimens were dissected by H. Bertsch, radula slides #172 (spm #1) and #173 (spm #2), but the latter is largely destroyed and uninformative; labial cuticles were missing]; Panama. Caribbean Sea, Canal Zone, Galeta Marine Laboratory, reef flat, 4 August 1974, one specimen 25/17 mm preserved, leg. H. Bertsch, identified as *Discodoris evelinae* by H. Bertsch (CASIZ 010575) [specimens were dissected by H. Bertsch, radula slide #125, but the radula is largely destroyed and uninformative; the labial cuticle was missing]; Panama, Caribbean Sea, Canal Zone, Galeta Island, 30 July 1974, two specimens 40/25 (#1) and 26/15 (#2) mm preserved, leg. H. Bertsch, identified as *Discodoris evelinae* by H. Bertsch (CASIZ 010577) [specimens were dissected by H. Bertsch; no slides could be found; labial cuticles were missing]; Panama, Caribbean Sea, Canal Zone, Galeta Island, reef flat, 19 August 1974, one specimen 29/20 mm preserved, leg. H. Bertsch, identified as *Discodoris evelinae* by H. Bertsch (CASIZ 010580) [specimen was dissected by H. Bertsch, radula slide #168; labial cuticle was missing]; Panama, Caribbean Sea, Canal Zone, Galeta Island, reef flat, 14 August 1974, two specimens 40/30 (#1) and 25/17 (#2) mm preserved, leg. H. Bertsch, identified as *Discodoris evelinae* by H. Bertsch (CASIZ 010581) [specimens were dissected by H. Bertsch; radula slide #164 and #165, but the specimens had not been numbered by Bertsch]; **Brazil**, Bahia, Itapoa Farrol, two specimens 35/20 (#1) and 30/15 (#2) mm preserved, 30 July 1975, leg M. P. Morse, identified as *Discodoris evelinae* probably by Ev. and Er. Marcus (MCZ 288294) [these specimens, originally part of the Marcus' collection, were examined prior to the present study; the notum was cut into pieces]; Brazil, PE, Suape, 25 August 1980, three specimens 55/35 (#1), 53/30 (#2), and 36/25 (#3) mm preserved, leg. Rosa de Lima Mello, identified as *Discodoris evelinae* by Ev. Marcus (MZSP 37929) [these specimens, part of the Marcus' collection (#131), are not vouchers; the specimen #1 was cut into pieces prior to the present study; its buccal mass is missing; its reproductive system was dissected by Ev. Marcus, but the penis was still present].

DISTRIBUTION.— Caribbean Sea and tropical western Atlantic Ocean, from Florida to São Paulo, Brazil. Florida (Marcus and Marcus 1967a, as *evelinae* and *hedgpethi*; present study), Bahamas (Redfern 2001; present study), Texas (Marcus and Marcus 1960b, as *hedgpethi*; present study), Puerto Rico (Marcus and Marcus, 1970a, as *hedgepthi*), Virgin Islands (Mörch 1863, as *crucis*; present study), Panama (Bertsch 1976, as *evelinae*; Meyer 1977, as *evelinae*; present study), Island of Santa Marta, off Colombian coasts (Marcus 1976a, as *evelinae*), Barbados (Marcus and Hughes 1974, as *evelinae*), Guadeloupe (Bergh 1877a, as *notha*; present study), and Brazil (MacFarland 1909, as *branneri*; Marcus 1955, as *evelinae*; Marcus and Marcus 1969b, as *evelinae*; Marcus 1970, as *evelinae*; present study). Note that *branneri* was recorded from the Grand Cayman Island under the name *evelinae* (Hess and Abbott 1994). However, the presence of *branneri* in the Cayman islands is still uncertain because *branneri* may be confused easily with *lilacina* (see this species) and the description provided by Hess and Abbott (e.g., rose-orange, brown or greenish—brown with darker spots) is vague and potentially compatible with both species.

WWW.— Anne DuPont posted (website: *Opisthobranchs from around the world*) a picture of a 12 mm long specimen (alive) identified as *Discodoris evelinae*. This specimen was collected by Ross W. Gundersen from St Ann's Bay, Jamaica, under a bed of *Thalassia*, at 2 meters depth, on October 9, 2003. My guess (which would have to be verified by a dissection) is that this specimen is part of *Tayuva lilacina*, not *evelinae*. Anne DuPont also posted (website: *Opisthobranchs from around the world*) another 12 mm long (alive) identified as *Discodoris evelinae*. This second specimen was collected by Anne DuPont from Lake Worth Lagoon, West Palm Beach, Florida, at 5 meters depth, on April 27, 2004. This specimen could be part of *branneri*, but it also could be part of *lilacina*.

OCCURENCE.— It does not seem to be rare, based on frequent specimen collections.

HABITAT.— Under rocks, in the intertidal zone or a few meters depth.

LITERATURE.— Several authors have provided some information about the color and the morphology of the dorsal notum of living animals (e.g., Marcus 1955, 1970; Marcus and Marcus 1960b, 1967a; Marcus and Hughes 1974). A color picture of a light brown animal identified as *Discodoris evelinae* is available in Humann (1992). Another color picture of a light reddish-brownish specimen can be found in Redfern (2001). The identified might be correct. Several authors have provided information about the internal anatomy. The three original descriptions (MacFarland 1909; Marcus 1955; Marcus and Marcus 1960b) are probably the most complete, although they are only based on one, two, and three specimens, respectively. Some additional data on the radula and the penial morphology can be found in several other publications (Marcus 1970; Marcus and Marcus 1967a, 1969b, 1970a, 1976a; Marcus and Hughes 1974). Bertsch (1976) analyzed in detail the infra-specific variation of the radular formula among specimens from the Atlantic coasts of Panama (as *evelinae*). Several authors have mentioned the species name *branneri* (Marcus 1955; Marcus and Marcus 1967a; Gohar and Soliman 1967) or discussed its supra-specific affinities (Perrone and Doneddu 1997), without adding new material. Bergh (1884a) simply mentioned the name *notha* in a list of *Discodoris* species.

REMARKS ON THE ORIGINAL DESCRIPTION (*branneri*, Figs. 241, 242A-D).— The original description of *branneri* by MacFarland is complete and accurate. MacFarland described (1909:66) a "dorsum pinkish, with thickly scattered irregular blotches of brown everywhere over its surface. Along the sides of the dorsum is a longitudinal row of five or six larger black spots about equidistant from each other." The notum is currently whitish. Observations of the notum with SEM confirmed that *branneri* does not bear caryophyllidia. The apex of some tubercles may be heavily ciliated, as in *Tayuva*. The oral tentacles are not grooved. The labial cuticle is covered with jaw rodlets. The radular formula is 26 × (45/48-0-45/48). All teeth have more or less the same size, except for the two or three innermost and outermost ones, which are smaller. All teeth are hamate. More importantly, MacFarland described the penial hooks covering the entire penis. The description of the penis itself, however, is confusing. Indeed, it is described (1909:66) as "nearly spherical, about 2.25 mm in diameter" and as a "large conical glans projecting externally." However, as MacFarland pointed out, the penis was retracted. According to MacFarland, the length of the hooks varies from 20 to 27 μm, but several hooks measured up to 40 μm. MacFarland pointed out that the length of the hooks approximately equal their diameter. However, this is probably biased by the fact that the penis was cut in transversal slices (and so the hooks could not be observed completely). Some of them clearly are curved cones, longer than wide. In all specimens of *branneri* dissected, a few large hooks were found at the base of the penis. Those hooks may have been lost during the dissection or the preparation by MacFarland. Another explanation that cannot be excluded is that the penis was not fully mature, without basal hooks. This, however, is unlikely because MacFarland described a fully mature reproductive system and because large basal hooks were found even in very small penises (see below). Finally, MacFarland represented a bursa copulatrix much larger than the receptaculum seminis, at least seven times.

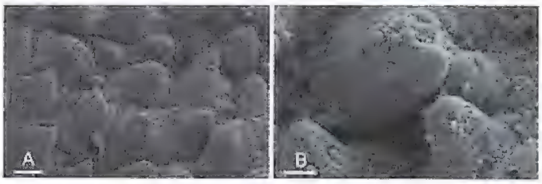

FIGURE 241. *Discodorididae branneri*, holotype, dorsal notum. A. Tubercles, scale = 100 μm.— B. Tubercles, scale = 40 μm.

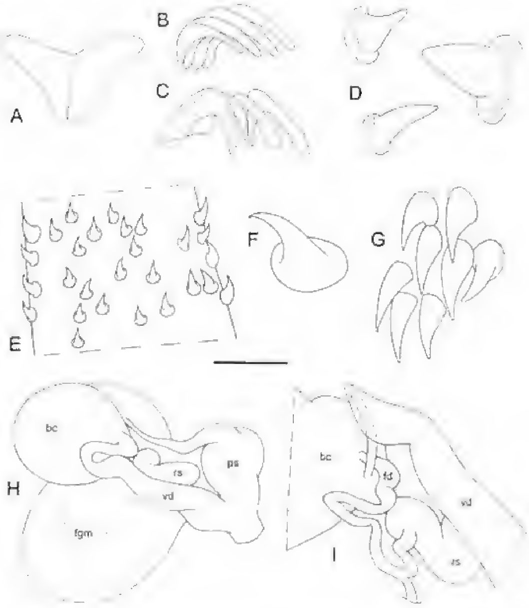

FIGURE 242. *Discodorididae branneri*, original descriptions and types. A. Jaws, *Discodoris branneri*, holotype, slide #021009, scale = 1 mm.— B. Outermost radular teeth, *Discodoris branneri*, holotype, slide #021009, scale = 170 μm.— C. Innermost radular teeth, *Discodoris branneri*, holotype, slide #021009, scale = 100 μm.— D. Penial hooks, holotype, slide #021009, scale = 20 μm.— E. Penial hooks, *Discodoris spetteda*, holotype, slide F-855, scale = 100 μm.— F. Penial hooks, base of penis, *Discodoris spetteda*, holotype, slide F-855, scale = 70 μm.— G. Penial hooks, original description of *Discodoris hedgpethi*, after Marcus and Marcus (1960a: fig. 11).— H. Reproductive system, paralectotype (specimen #3) of *Doris crucis*, scale = 3.3 mm.— I. Spermatic pouches, paralectotype (specimen #3) of *Doris crucis*, scale = 1.5 mm.

REMARKS ON THE ORIGINAL DESCRIPTION (*evelinae*).— Marcus (1955) described in detail the external morphology, e.g., notum covered with conical tubercles of different sizes irregularly distributed, rhinophores with 25/30 lamellae, oral tentacles conical, not grooved. The color of the living animals was "olivaceous brown with darker blotches on the back and lighter with large dark spots below." (Marcus 1955:143) The labial cuticle is covered with jaw rodlets. The radular formula is 35 × (70/80-0-70/80). All lateral teeth have more or less the same size, except the two or three innermost and outermost ones, which are smaller. All teeth are hamate and bear no denticles. The description of the penial hooks is ambiguous. Indeed, Marcus described a 3 mm long penis covered with 0.18 mm long penial hooks. However, the size of the penial hooks of *branneri* (see below) varies a great deal: the basal hooks measure from 100 up to almost 300 µm, and all other hooks measure 45-50 µm in average. Given that the hooks present in the holotype of *branneri* and the hooks illustrated by Marcus for *evelinae* have a similar shape, it is likely that MacFarland did not mention the basal hooks and that Marcus only mentioned those larger hooks. Note that Marcus compared *evelinae* with *branneri* but did not regard the different sizes of the penial hooks as a difference between the two species, at least in the original description (see discussion). Finally, Marcus represented a bursa copulatrix six or seven times larger than the receptaculum seminis. The latter is clearly elongated and folded upon itself.

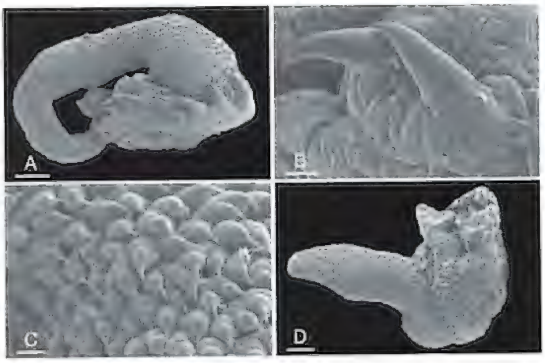

Figure 243. *Discodorididae branneri*, penis, syntypes of *hedgpethi*, MZSP 37968. A. One of the three syntypes, scale = 400 µm.— B. Proximal penial hooks (same penis as A), scale = 100 µm.— C. Penial hooks (same penis as A), scale = 50 µm.— D. Another syntype, scale = 200 µm.

Remarks on the original description (*hedgpethi*, Figs. 242G, 243).— The original description of *hedgpethi* is similar to the description of *evelinae*, but less detailed. Marcus and Marcus (1960b) described the external morphology, e.g., notum covered with conical tubercles of different sizes irregularly distributed, rhinophores with 25 lamellae, oral tentacles conical and not grooved. The dorsal color of live animals was "pale olive green with black spots and blotches, up to 3 mm in diameter; the sole of the foot is less spotted." (Marcus and Marcus 1960b:143) The labial cuticle is covered with jaw rodlets. The radular formula is 26 × (44-0-44). All lateral teeth have more or less the same size, except for the two or three innermost and outermost ones, which are smaller. All teeth are hamate and bear no denticles, with the exception of the first innermost tooth whose cusp, according to Marcus and Marcus, bears a denticle. However, their drawing representing these denticles is not precise and it is difficult to determine what they actually saw. In any case, it seems that the authors did mention this feature again in any new individuals after the original description (e.g., Marcus and Marcus 1967a). The penial hooks of the types of *hedgpethi*, *evelinae*, and *branneri* all have a similar shape. Marcus did not specify their size. The hooks of the penis mounted for the present study are similar to the hooks found in all other specimens of *branneri*: the basal large hooks measure up to 300 µm and the other hooks measure 50 µm in average. Marcus and Marcus did not mention the penis sizes: the two penises prepared here measure 2 and 3 mm in length. Finally, the bursa copulatrix is much larger (at least ten times) than the pear-shaped receptaculum seminis.

Morphological description and variation of new specimens (including paralectorypes of *crucis* and *notha*, Figs. 242E-F, H-I, 244-257).— *Color*. The live color of animals dissected is unknown. All preserved specimens share a similar color. The ground color of the dorsal notum is whitish to light brown, and bears wide and irregular dark spots, some of which (the large ones) may be arranged in two longitudinal rows between the rhinophores and the gills. Note that preservation lightens those dark spots in most specimens. It may even remove them. The ventral surface (hyponotum and foot) is creamish, with dark brown dots.

External morphology. The body is oval. The length equals less than twice the width. The largest specimen was 60 mm long, preserved. The foot is rounded posteriorly and anteriorly. The width of the foot equals about one third or one half of the width of the dorsal notum (in preserved specimens). The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, but not grooved. The dorsal notum bears tubercles that are not caryophyllidia. Many small holes (diameter < 10 μm) and many tufts of cilia were found on the dorsal notum. Many tubercles have a ciliated apex, exactly as in caryophillidia, except that it is not surrounded by a regular circle of spicules. In preserved specimens, the margins of the rhinophoral and branchial sheaths can be smooth or crenulate. There are six wide tetra- or tripinnate branchial plumes. The rhinophores have from 20 to 35 lamellae (usually between 25 and 30).

Digestive system. The stomach is large, free, on top of the left anterior side of the digestive gland. A small caecum is present. The length of the intestine varies: straight and dorsal (e.g., CASIZ 010576, CASIZ 010580, CASIZ 072292); with a few loose, dorsal loops (e.g., CASIZ 010570, MCZ 288294); with a loop on the right ventral side of the digestive gland (e.g., ZMUC GAS-2126, CASIZ 010577). The labial cuticle is armed with a pair of sickle-shaped jaw plates. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. Radular formulae were: 22 × (53-0-53) in a 30 mm long specimen (MCZ 288294 #2), 23 × (50/53-0-50/53) in a 29 mm long specimen (CASIZ 010580), 24 × (45/48-0-45/48) in a 27 mm long specimen (CASIZ 010571), 24 × (49-0-49) in a 38 mm long specimen (CASIZ 072292 #2), 24 × (56/58-0-56/58) in a 25 mm long specimen (CASIZ 010581 #2), 26 × (55-0-55) in a 53 mm long specimen (type *crucis* #3), 26 × (58/62-0-58/62) in a 40 mm long specimen (CASIZ 010581 #1), 27 × (54-0-54) in a 45 mm long specimen (CASIZ 072292 #1), 27 × (58-0-58) in a 35 mm long specimen (MCZ 288294 #1), 28 × (45/50-0-45/50) in a 36 mm long specimen (ZMUC GAS-2126 #2), 28 × (50/53-0-50/53) in a 40 mm long specimen (CASIZ 010570 #2), 28 × (58/61-0-58/61) in a 45 mm long specimen (CASIZ 010570 #1), 32 × (57/62-0-57/62) in a 60 mm long specimen (CASIZ 010572 #1). The rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth gradually increases towards the edge of the radula except for the three or five outermost teeth of which the size decreases gradually. All teeth are hamate, including the outermost ones, although the base of the last outermost tooth can be reduced. The teeth are not grooved and bear no denticles.

Nervous system. The length of the circum-esophageal nerve ring equals up to three times the width of the cerebro-pleural ganglia. The cerebral and pleural are more or less fused. They may be separate from the pedal ganglia or fused with them. The surface of the ganglia is smooth.

Reproductive system. The ampulla is convoluted (from two loose loops to many tight loops). The division between male and female ducts (hidden within the female gland mass) could not be seen by dissection. The prostate is divided in a proximal whitish part and a distal yellowish-orange part. The deferent duct is usually straight, although it can be loosely convoluted (with one loose loop) near the penial sheath. The deferent duct ends in a distinct, permanent penis. The penis is covered with hooks (except at the apex) which all have the shape of a curved cone. The length of the penial hooks varies depending on their position: a few basal (proximal) hooks measure from 100 up to 300 μm. In several specimens, one of those basal hooks was found to be larger than the others. Also, an exceptionally large basal hook (450 μm long) was found in the smallest penis (MCZ 288294 #2), which suggests that the large basal hooks may appear in the early stages of the development of the penis. The length of the hooks present on the rest of the surface of the penis ranges from 30 to 70 μm. The hooks are randomly placed on the surface. Their density and size tend to decrease gradually towards the apex. Note that the apex of the hooks is oriented towards the base

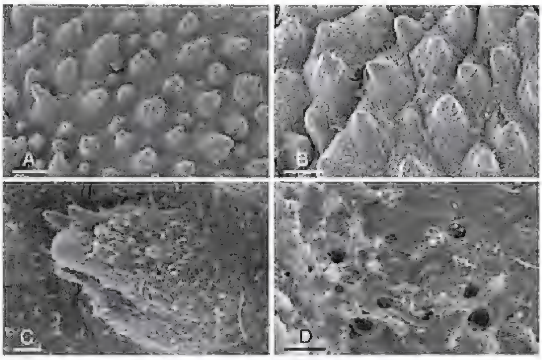

FIGURE 244. *Discodorididae branneri*, dorsal notum. A. Tubercles, CASIZ 072292 (#2), scale = 200 µm.— B. Tubercles, CASIZ 072292 (#1), scale = 200 µm.— C. A tubercle, CASIZ 072292 (#2), scale = 40 µm.— D. External surface of the dorsal notum, detail, CASIZ 072292 (#1), scale = 20 µm.

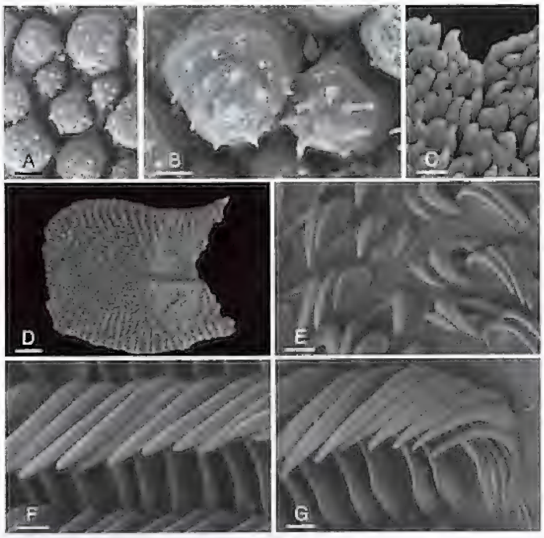

FIGURE 246. *Discodorididae branneri*, paralectotype of *notha*, ZMUC 2126 (#2). A. Dorsal notum, tubercles, scale = 100 µm.— B. Dorsal notum, tubercles, scale = 60 µm.— C. Jaw rodlets, scale = 10 µm.— D. Radula, scale = 400 µm.— E. Innermost teeth, scale = 40 µm.— F. Median teeth, scale = 40 µm.— G. Outermost teeth, scale = 30 µm.

of the penis. The penis measures from 1.7 to 11 mm in length: 1.7 mm in a 30 mm long specimen (MCZ 288294 #2), 2.5 mm in 36 mm long specimen (MZSP 37929 #3), 2.7 mm in 55 mm long specimen (MZSP 37929 #1), 3 mm in a 38 mm long preserved specimen (CASIZ 072292 #2), 3.3 mm in a 53 mm long specimen (*crucis*, type #3), 3.4 mm in a 45 mm long preserved

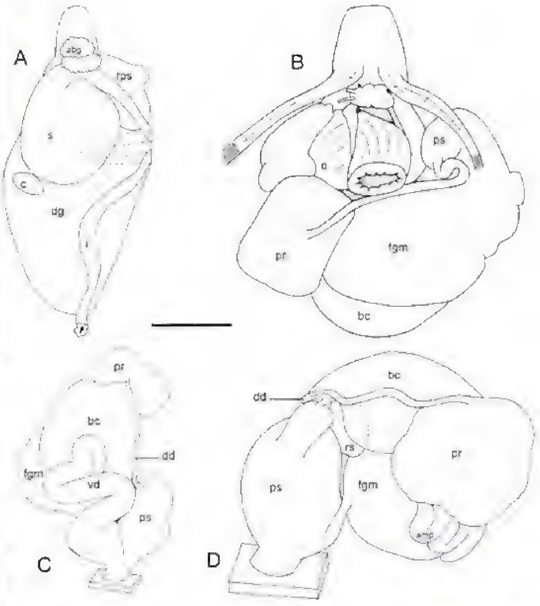

FIGURE 245. *Discodorididae branneri*, paralectotype of *Discodoris notha* (ZMUC 2126, spm #2). A. General anatomy, scale = 8 mm.— B. Anterior anatomy, buccal mass, nervous system, and reproductive system, scale = 3.5 mm.— C. Reproductive system, scale = 3.7 mm.— D. Reproductive system, scale = 3.8 mm.

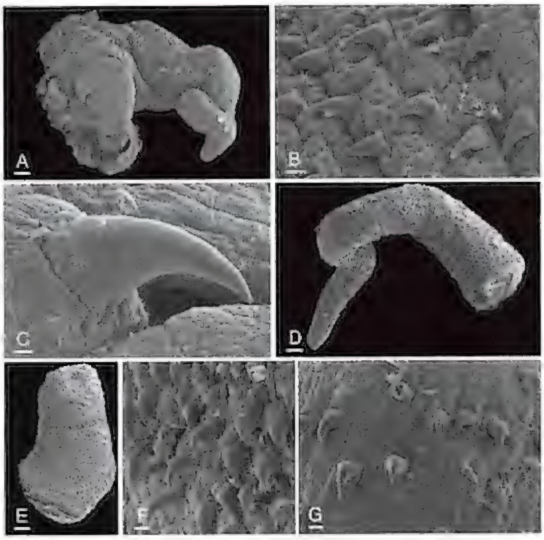

FIGURE 247. *Discodorididae branneri*, penis, paralectotypes of *Discodoris notha*. A. ZMUC 2126 (#2), scale = 200 µm.— B. Penial hooks, ZMUC 2126 (#2), scale = 20 µm.— C. Large basal hook, ZMUC 2126 (#2), scale = 20 µm.— D. ZMUC 2126 (#1), scale = 200 µm.— E. ZMUC 2126 (#1), scale = 100 µm.— F. Penial hooks, ZMUC 2126 (#1), scale = 20 µm.— G. Penial hooks, ZMUC 2126 (#1), scale = 20 µm.

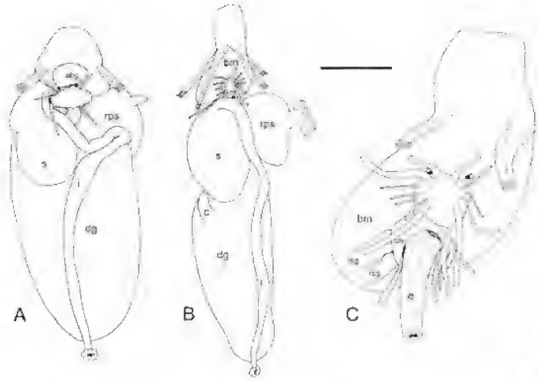

FIGURE 248. *Discodorididae branneri*. A. General anatomy, MCZ 288294 (#1), scale = 6 mm.— B. General anatomy, CASIZ 072292 (#2), scale = 5 mm.— C. Buccal mass and nervous system, scale = 1.4 mm.

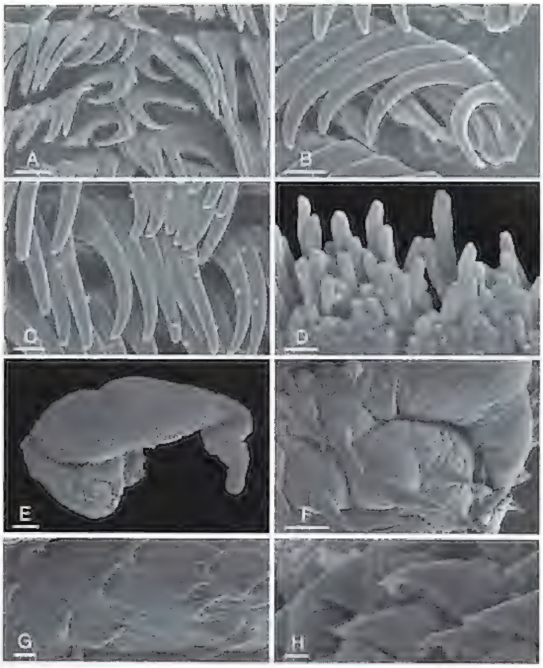

FIGURE 249. *Discodorididae branneri*, paralectotype #3 of *crucis*, ZMUC. A. Innermost teeth, scale = 30 µm.— B. Outermost teeth, scale = 30 µm.— C. Median teeth, scale = 30 µm.— D. Jaw rodlets, scale = 10 µm.— E. Penis, scale = 200 µm.— F. Proximal penial hooks, scale = 100 µm.— G. Penial hooks, scale = 30 µm.— H. Penial hooks, scale = 10 µm.

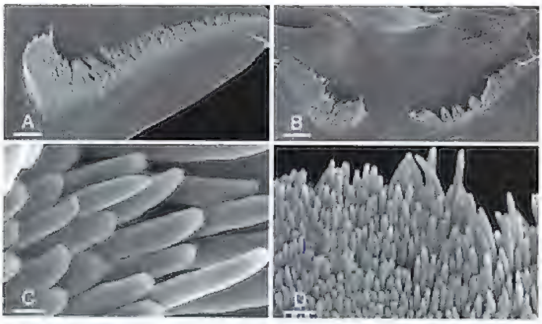

FIGURE 250. *Discodorididae branneri*, labial cuticle. A. One lateral jaw plate, CASIZ 072292 (#2), scale = 100 µm.— B. A pair of lateral jaw plates, CASIZ 072292 (#1), scale = 100 µm.— C. Jaw rodlets, CASIZ 072292 (#2), scale = 5 µm.— B. Jaw rodlets, CASIZ 072292 (#1), scale = 20 µm.

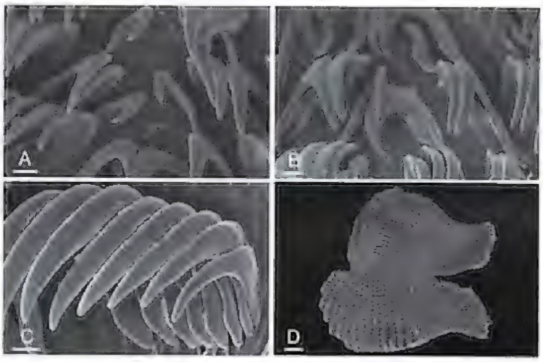

FIGURE 251. *Discodorididae branneri*, radula. A. Innermost teeth, MCZ 288294 (#1), scale = 20 µm.— B. Innermost teeth, MCZ 288294 (#2), scale = 20 µm.— C. Outermost teeth, CASIZ 072292 (#2), scale = 20 µm.— D. CASIZ 072292 (#1), scale = 300 µm.

specimen (CASIZ 072292 #1), 4 mm in 53 mm long specimen (MZSP 37929 #2), 4.2 mm in a 35 mm specimen (MCZ 288294 #2), 4.5 mm in a 25 mm specimen (CASIZ 010581), 5 mm in a 26 mm long specimen (CASIZ 010577 #2), 5 mm in a 36 mm specimen (ZMUC GAS-2126, dissection for the present study), 5 mm in a 27 mm specimen (CASIZ 010571), 5 mm in a 25 mm specimen (CASIZ 010575), 6 mm in a 45 mm specimen (ZMUC GAS-2126 #1, Bergh's dissection), 6 mm in a 29 mm specimen (CASIZ 010580) and in a 41 mm specimen (CASIZ 010581), 6.5 mm in a 60 mm specimen (CASIZ 010572 #1), 11 mm in a 56 mm specimen (USNM 576292). The base of the penis is protected within the penial sheath, and the rest of the penis retracts within the vaginal duct. The latter is broad and loosely convoluted up to the bursa copulatrix. The fertilization duct is short and sometimes convoluted (two or three loose loops). The disappearance of the fertilization duct into the female gland mass is marked by a short, distinct duct. The duct of the receptaculum seminis is long (about half of the length of the receptaculum seminis itself). The bursa copulatrix, more or less spherical, is much larger than the receptaculum seminis (up to ten times, usually about six times). The receptaculum seminis is elongated (sausage-shaped) in most specimens. It may be folded upon itself depending on its arrangement. Its surface is smooth, although sometimes it presents some small protuberances.

Diagnostic features.— The best diagnostic character of *branneri* is its penis. The color of live animals seems to vary a great deal (see discussion) and *branneri* may be misindentified as *hummelincki*, which has a similar distribution (see *lilacina*, Caribbean Sea). However, these two species will probably be distinguishable when more information is available about the color variation of both *branneri* and *lilacina* (in the Caribbean). It would be premature to provide a criterion that could be used in the field.

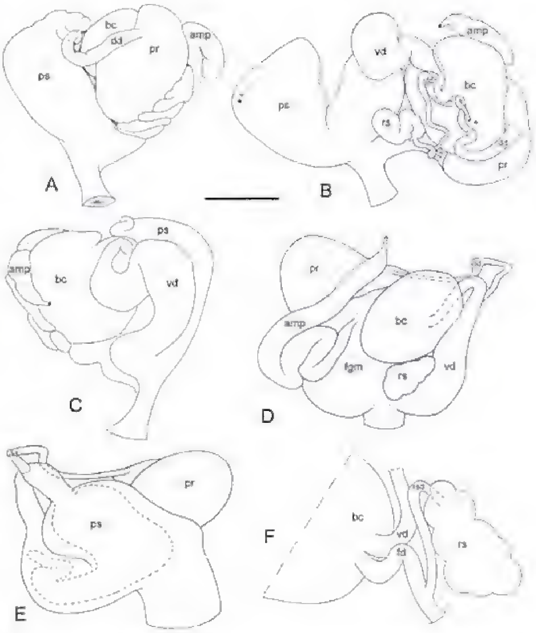

FIGURE 252. *Discodorididae branneri*, reproductive system. A. CASIZ 072292, scale = 3.5 mm.— B. Deferent duct cut and organs separated, CASIZ 072292, scale = 3.5 mm.— C. CASIZ 072292, scale = 4 mm.— D. MCZ 288294 (#1), scale = 3.5 mm.— E. MCZ 288294 (#1), scale = 4 mm.— F. Spermatic pouches, MCZ 288294 (#1), scale = 3 mm.

Infra-specific character variation.— Dark blotches and spots are always present on the dorsal notum, as well as dots on the ventral surface. However, the ground color may vary: olivaceous brown (Marcus 1955, as *evelinae*), pale olive (Marcus and Marcus 1960b, as *hedgpethi*), dull (Marcus and Marcus 1967a, as *evelinae*), pale rose orange (Marcus and Marcus 1967a, as *evelinae*), pink (Marcus and Marcus 1969b, as *evelinae*), pink and cream (Marcus and Hughes 1974, as *evelinae*). Anatomical and morphological data available in the literature are fully compatible with observations provided here. The largest live animals measured 108 mm (Marcus and Marcus 1970a, as *hedgpethi*) and 90 mm (Marcus and Marcus 1967a, as *evelinae*). After preservation, the 108 mm long live animal measured 85 mm. The 60 mm long specimen, preserved, from Panama (CASIZ 010572 #1) probably measured about 80/90 mm alive. Bertsch (1976) addressed thoroughly the individual variation of the radula within *branneri* (as *evelinae*) based on a series of specimens from Panama (some of which have been re-examined in the present study) and the literature published prior to 1976. The range of variation he found was as follows: the number of rows varies from 16 (for 25 teeth per half row) in a 18 mm long specimen (alive) up to 50 (for 80 teeth per half row) in a 108 mm long specimen (alive). Let us just add to Bertsch's thorough analysis that Marcus and Marcus (1969b) described a formula of 36 × (84-0-84) in a 65 mm long specimen. Comparing the different reproductive systems that have been described with new observations is difficult because the drawings published so far are too schematic. However, they are compatible with observations provided here, including for the relative size of the spermatic pouches and the length of the spermatic ducts. The penis sizes found in the literature range from 1.8 to 11 mm: 1.8 mm in a 25 mm long specimen (Marcus and Marcus 1970a, as *hedgpethi*), 3 mm in a 27.5 mm long specimen (Marcus and Marcus 1970a, as *hedgpethi*), 4.5 mm in a 35 mm long specimen (Marcus 1970,

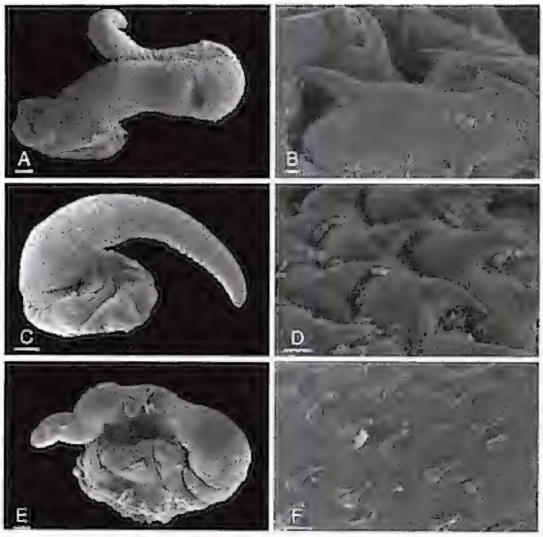

FIGURE 253. *Discodorididae branneri*, penis. A. CASIZ 010571, scale = 200 µm.— B. Penial hooks, CASIZ 010571, scale = 30 µm.— C. CASIZ 010572 (#1), scale = 400 µm.— D. Penial hooks, CASIZ 010572 (#1), scale = 10 µm.— E. CASIZ 010580, scale = 200 µm.— F. Penial hooks, CASIZ 010580, scale = 20 µm.

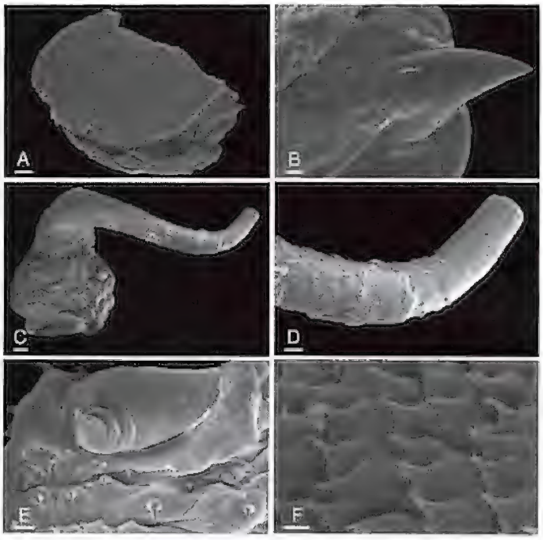

FIGURE 254. *Discodorididae branneri*, penis. A. CASIZ 072292 (#1), scale = 200 µm.— B. Large, proximal penial hook, CASIZ 072292 (#1), scale = 30 µm.— C. CASIZ 010577 (#2), scale = 200 µm.— D. Apex, CASIZ 010577 (#2), scale = 100 µm.— E. Penial hooks, CASIZ 010577 (#2), scale = 100 µm.— F. Penial hooks, CASIZ 010577 (#2), scale = 20 µm.

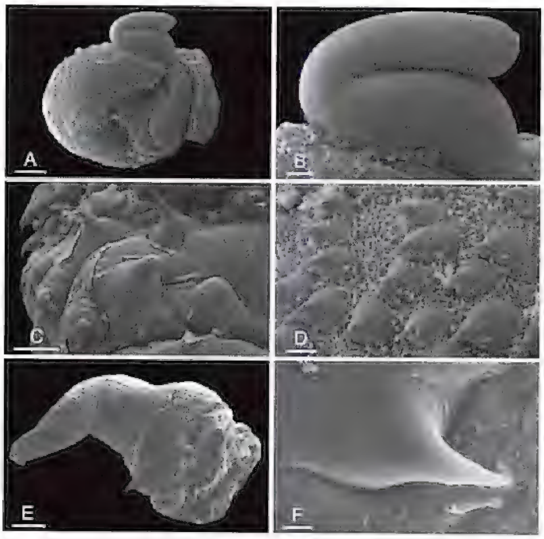

FIGURE 255. *Discodorididae branneri*, penis. A. MCZ 288294 (#1), scale = 300 µm.— B. Smooth apex, MCZ 288294 (#1), scale = 100 µm.— C. Penial hooks, MCZ 288294 (#1), scale = 100 µm.— D. Penial hooks, MCZ 288294 (#1), scale = 30 µm.— E. MZSP 37929(#2), scale = 500 µm.— F. Penial hook, MZSP 37929(#2), scale = 5 µm.

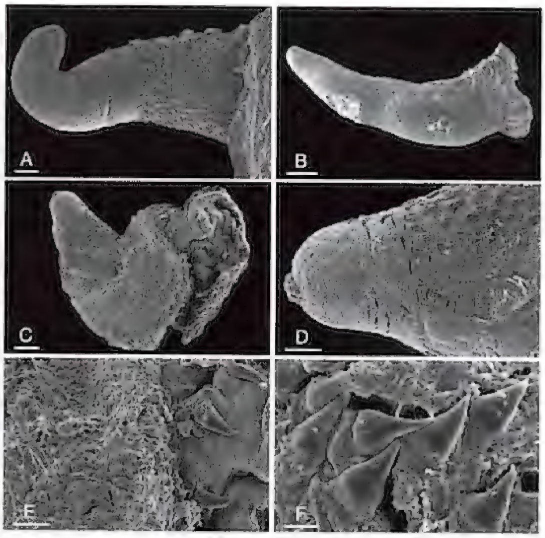

FIGURE 256. *Discodorididae branneri*, penis. A. MZSP 37929(#1), scale = 200 µm.— B. MZSP 37929(#3), scale = 200 µm.— C. CASIZ 072292 (#2), scale = 200 µm.— D. Apex, CASIZ 072292 (#2), scale = 100 µm.— E. Penial hooks, CASIZ 072292 (#2), scale = 100 µm.— F. Penial hooks, CASIZ 072292 (#2), scale = 20 µm.

as *evelinae*), and 11 mm in a 55 mm specimen (Marcus and Marcus 1967a, as *hedgpethi*) and a 85 mm specimen (Marcus and Marcus 1970a, as *hedgpethi*). In summary, the penis length varies from 1.7 (present study) to 11 mm. Note that the length of a preserved penis varies due to natural polymorphism among individuals, but also because of preservation and fixation (e.g., retraction of the penis when the animal is put in alcohol or formalin), which explains why the penis length is not necessarily related to the size of the animal itself. So far, the maximum size of the basal hooks was 250 µm, but several 300 µm long hooks and even one 450 µm long hook were found. MacFarland (1909) mentioned the smallest penial hooks (20 µm); their length ranges from 30 to 70 µm.

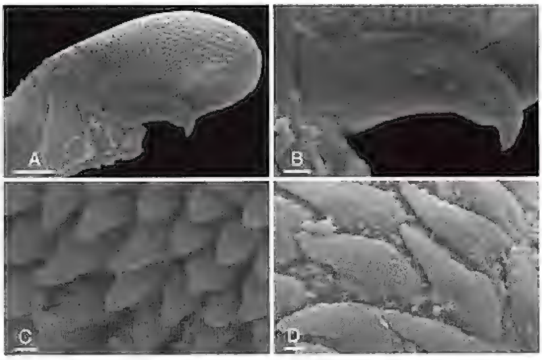

FIGURE 257. *Discodorididae branneri*, penis. A. MCZ 288294 (#2), scale = 200 µm.— B. Large proximal hook, MCZ 288294 (#2), scale = 50 µm.— C. Penial hooks, MCZ 288294 (#2), scale = 10 µm.— D. Penial hooks. MCZ 288294 (#2), scale = 10 µm.

DISCUSSION.— The case of *branneri* illustrates perfectly what taxonomy should not be: the creation of new species names without any understanding of character variation. Marcus (1955) discussed the existence of *branneri* when he created the new species name *evelinae*. Both species were described from the Brazilian coasts, on the basis of one specimen for *branneri* and two specimens for *evelinae*. The only difference between these specimens was the number of teeth per half row: 35 × (77/80-0-77/80) for *evelinae* and 26 × (45/48-0-45/48) for *branneri*. The two reproductive systems slightly differed but the "principles [were] the same" (Marcus 1955:145): the two systems only differ for minor details such as the relative size of female and male structures which, as Marcus admitted, change depending on the stage of maturation of the individuals. Because the reproductive system of the holotype of *branneri* was cut in histological sections, the drawings of Marcus (1955) and MacFarland (1909) can hardly be compared. However, they are compatible. Marcus (1955) mentioned that *branneri* had "cuticular hooks on the verge, like *D. evelinae*," but, surprisingly, he did not consider that this important feature as a sign that the three specimens were part of the same species. Interestingly, Marcus (1955) did not discuss the difference of size between the hooks described by MacFarland (20 to 27 µm) and by him (180 µm). However, our current knowledge on the penial morphology of *branneri* (see above) shows that the size of the hooks actually varies from 30 µm distally up to 300 µm (exceptionally 450 µm) proximally. Marcus (1955) also compared *evelinae* with *Discodoris voniheringi*, which belongs to *Discodorididae* as well, another species described by MacFarland (1909) from the coasts of Brazil. However, as pointed out by Marcus, *evelinae* and *voniheringi* are easily distinguishable because the penis of *voniheringi* is unarmed.

Four years later, Marcus and Marcus (1960b) described another species whose penis was bearing penial hooks too, *hedgpethi*, based on three specimens collected from Texas. They compared *hedgpethi* with both *branneri* and *evelinae*. According to them, *branneri* was closer to *hedgpethi* than to *evelinae*: the latter had a higher number of teeth per half row (72-82 teeth) than the two other species (44 in *hedgpethi*, 45-48 in *branneri*). Marcus and Marcus distinguished *hedgpethi* from *branneri* based on: 1) the length of the esophagus (short and wide in *branneri*, long and narrow in *hedgpethi*); 2) the size of the bursa copulatrix (Marcus and Marcus mentioned that it "may be" less distended in "the specimen of *hedgpethi* examined"); 3) the penial hooks (equal length and basal diameter in *branneri*, longer than wide in *hedgpethi*); 4) the maximum length of the labial rodlets (96 μm in *branneri*, 150 μm in *hedgpethi*); 5) the presence of broadened cusp of the innermost radular teeth in *hedgpethi*. All these distinctions, however, simply are the result of insufficient sampling of (a total of six specimens for three species). Moreover, Marcus did not mention that the shape of the penial hooks described by MacFarland was similar to the ones they illustrated, which should have warned them that all those specimens could be part of the same species.

The next step in the discovery of *branneri* was the mention of three specimens by Marcus and Marcus (1967a), all from Florida, but two as *evelinae* and one as *hedgpethi*. The key of identification they came up with is as follows: half row with a mininum of 71 teeth (*evelinae*); half-row with a maximum of 53 teeth, rachis of radula deeply grooved longitudinally, and penis of adult 4 mm long with hooks up to 0.027 mm in height (*branneri*); half-row with a maximum of 53 teeth, rachis of radula with longitudinal fold, and penis of adult 11 mm long with hooks up to 0.25 mm in height (*hedgpethi*). Again, this key did not consider the possibility of individual variation, especially concerning the penis length and the radular formula. In some of the specimens dissected, a "rachidian fold" was observed, but this was always a subtle and, actually, meaningless feature. The lack of large basal hooks in the penis of the holotype of *branneri* is commented on above (see remarks on the origininal description of *branneri*). More importantly, the specimen described as *hedgpethi* by the Marcus (USNM 576292) was re-examined. This specimen was mentioned by Marcus and Marcus (1966) as *Discodoris spetteda*, a *nomen nudum*. The drawings that Marcus and Marcus (1967a:77, figs 98D-E) published for the penis of this specimen are inaccurate: there are much fewer hooks covering the penis than what they represented.

Then Marcus (1970) and Marcus and Marcus (1969b, 1970a) continued to describe a few specimens under the two names *evelinae* and *hedgpethi*, until they finally decided that, given the individual variation of the radular formula, *hedgpethi* should be a synonym of *evelinae*. However, *branneri*, which Marcus and Marcus (1960b) considered to be closer to *hedgpethi* than to *evelinae*, was suddenly forgotten. It is now clear that all the differences that have been mentioned between *branneri*, *evelinae* and *hedgpethi* result from the fact that the Marcuses ignored individual character variation.

Finally, the presence of a *branneri*-like penis in some types of *notha* and *crucis* was never pointed out in the literature because the original descriptions of these species do not mention an armed penis, and the types have not been re-examined since Bergh's original description.

Supra-specific relationships.— Perrone and Doneddu (1997) proposed the transfer of *branneri* from *Discodoris* to *Carminodoris*. Most of the characters given by Perrone and Doneddu in the diagnosis of *Carminodoris* are actually symplesiomorphies of *Discodorididae*, such as digitiform oral tentacles, gills tri- or quadripinnate, radula with no rachidian teeth. The presence of an armed penis mentioned by Perrone and Doneddu in the diagnosis of *Carminodoris* is problematic because it does not take into account the fact that many other discodoridids have an armed penis. Finally, Perrone and Doneddu (1997) placed *evelinae* in the *Carminodoris* but did not mention the possible synonymy between *evelinae* and *branneri*. Interestingly, MacFarland (1909) rejected affinities of *branneri* with *Carminodoris* species because he thought that those had a different notum. In any case, *Carminodoris* also differ from *branneri* because it has an accessory gland in the reproductive system with a hollow spine.

A phylogenetic test of the relationships of *branneri* shows that *branneri* does not belong to *Carminodoris*. However, it does not belong to the clade *Discodoris*: it just is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial for *branneri* should be *"Montereina" branneri*. Possible names under the *ICPN* are *"Montereina" branneri* or simply *Discodorididae branneri*.

Future studies.— The color of live animals, especially its variation, obviously should be addressed. People will need pictures of the live animals combined with anatomy (in order to check the penial shape). A study of the development of the penis, and how spines arise would also be interesting, because we know little about this. Specimens from Florida and southern Brazil have a similar anatomy, but, as always, population studies could reveal cryptic species.

"*Montereina*" *coerulescens* (Bergh, 1888) New combination
Discodorididae coerulescens (Bergh, 1888) New combination

Figures 258-273.

Discodoris coerulescens Bergh, 1888:805-807, plate LXXXIII, figs 6-12.— Edmunds, 1971:349-352, fig. 5.
Discodoris ? *coerulescens*.— Eliot, 1909b:222-223.
Discodoris cf. *mauritiana*.— Coleman, 2001:56, unnumbered figure [not *Peltodoris mauritiana* Bergh, 1889].
Discodoris sp. Coleman, 2001:56, fig. "AMPI 249."
Doridacea sp. 7. Ono, 1999:140, fig. 234.

TYPE MATERIAL.— Two syntypes (ZMUC GAS-2132 & ZMB 43930): one specimen 17/11 mm preserved, leg. Moebius, [no collecting date] (ZMUC); one specimen 28/15 mm preserved, leg. Möbius, [no collecting date] (ZMB).

TYPE LOCALITY.— Mauritius.

TYPE MATERIAL CONDITION.— Both syntypes were dissected by Bergh. Only the mantle remains in both jars. No slides could be found.

ADDITIONAL MATERIAL DISSECTED.— **Madagascar**, 5 km West South West of Mora Mora Village, North East of pass through reef, 8 April 1989, one specimen 11/4 mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 161292); **Indian Ocean**, Seychelles, Aldabra Atoll, Passe Femme, 09°S, 46°E, 17 March 1986, one specimen 23/12 mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 074198); **Papua New Guinea**, North coast Madang, Cement Mixer Reef, approximately West North West of Rasch Pass in line with Ruo Island, 4 meters depth, 14 June 1992, one specimen 15/7 mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 086325); **Philippines**, Luzon Island, Batangas Province, Balayan Bay, Seafari Beach, 10 meters maximum depth, 24 February 1995, one specimen 25/13 mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 103713); Philippines, Mindoro, Sabang, La Laguna Munbi, point West of Sabang Resort, 1 March 1995, one specimen 21/12 mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 103712); Philippines, Luzon Island, Batangas Province, Balayan Bay, Ligpo Island, Ligpo dock, 10 meters maximum depth, 2 March 1995, one specimen 15/6 mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 105689); Philippines, Luzon Island, Batangas Province, Balayan Bay, Koala, 4 meters depth, T. M. Gosliner, 10 May 2001, one specimen 17/8 mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 157476); **Japan**, Ryukyu Islands, Okinawa, 1.3 km East North East of Maeki-zaki, Seragaki Beach, 26°30.4'N, 127°52.6'E, 2 meters depth, 17 February 1989, one specimen 20/12 mm preserved, leg. R. F. Bolland, identified as *Discodoris* by T. M. Gosliner (CASIZ 070167); **New Caledonia**, Secteur de Touho [Touho and surrounding area], September 1993, two specimens 24/15 (#1) and 15/9 (#2) mm preserved, leg. Montrouzier expedition (MNHN); **Pacific Ocean**, Cook Islands, Rarotonga Island, near Ava Avarua, 20 September 1984, one specimen 20/15 mm preserved, leg. G. Paulay, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 071702).

DISTRIBUTION.— Indo-Pacific. Tanzania (Edmunds 1971), Madagascar (present study), Mauritius (Bergh 1888), Seychelles (present study), Papua New Guinea (present study), Philippines (present study), Japan (present study), New Caledonia (present study), and Cook Islands (present study). Barnard (1927) mentioned the presence of *coerulescens* on the Natal coasts, but his identification is doubtful (see below). Some pictures published recently seem to be specimens of *coerulescens*: One individual was collected from Zamami Island, southern Japan (Ono 1999, as Doridacea sp.7); another one from Dampier, Western Australia (Coleman 2001, as Mildewed Discodoris, or *Discodoris* sp.); and a third individual from the Maldives, Indian Ocean (Coleman

2001, as *Discodoris* cf. *mauritiana*). One 12/3 mm specimen from the coast of Natal was identified as an immature of "perhaps" *D. coerulescens* by Eliot (1909b): it is not possible to determine what Eliot was looking at. One 8/5 mm specimen from Mauritius was identified as *Discodoris* cf. *coerulescens* by Yonow and Hayward (1991): it is not possible, based on the data published by the authors, to determine whether or not they actually saw *coerulescens*.

WWW.— The specimen identified as *Discodoris* cf. *mauritiana* posted on the *Opisthobranchs of the Kii Peninsula* is part of *coerulescens*. The 42 mm long specimen photographed in Okinawa on May 5, 1991, by Robert Bolland (see his website, 21 April 2003), and identified as *Discodoris* cf. *palma* Allan, 1933, could be part of *coerulescens* or *Tayuva lilacina*.

OCCURENCE.— It certainly is not a common species, but it is not rare either. In the field, it probably is often confused with other discodorid species, such as *Tayuva lilacina*, *Peltodoris murrea*, and young *Sebadoris fragilis*.

HABITAT.— Reef flat (CASIZ 161292), coral rubble (CASIZ 070167), under rocks (CASIZ 071702; Edmunds 1971; Coleman 2001, as *Discodoris* cf. *mauritiana*), under dead coral (Coleman 2001, as "Mildewed Discodoris").

LITERATURE.— Edmunds (1971) provided some information about the color of the dorsal notum of live animals, but no picture was published prior to this study. The specimens of *coerulescens* photographed in field guides (see above) were misidentified or not identified. Bergh (1888) and Edmunds (1971) described part of the internal anatomy, in particular the reproductive system and its peculiar hermaphroditic gland, independent from the digestive gland. However, infra-specific character variation was never addressed: only four individuals have been dissected so far (two by Bergh, and two by Edmunds). Eliot (1903:365) described a subspecies of *coerulescens*, *Discodoris caerulescens variegata*, but mentioned that he had not observed the independent hermaphroditic gland, which is a diagnostic character of *coerulescens*. It is likely that the specimen described by Eliot was not part of *coerulescens*. Eliot (1910a:422) briefly pointed out that *coerulescens* possesses a "remarkable structure of the hermaphroditic gland, which may be of generic importance." This specimen is not at the NHM, London, and is probably lost. Finally, Barnard (1927) recorded *coerulescens* from the Natal coast, but his identification can hardly be taken in consideration because he did not indicate how he re-identified *coerulescens*.

REMARKS ON THE ORIGINAL DESCRIPTION (Figs. 259B-C).— The color was originally described as "*coerulescente-albidus*; *rhinophoria clare lutea griseo maculata*" based on Moebius' brief field notes. This probably means that the color is whitish with bluish sheen, as it is found in other species, such as *Peltodoris murrea*. The syntypes currently are homogeneously light brown (ZMUC) and light witish (ZMB). The tubercles are embedded in a thick matrix, which is probably due to preservation but which also is a potential source of confusion with *murrea*. Bergh described some general features shared by all discodorids, such as the presence of digitiform oral tentacles, a bilabiate anterior foot with a notched superior lip. He also described some general morphological and anatomical features, such as 40 to 50 rhinophoral lamellae, a labial cuticle armed with two lateral jaw plates. The description of the radula is confusing. According to Edmunds (1971), the formula originally described by Bergh was 12/13 × (45-0-45). However, it seems that Bergh described a total number of rows ranging from 24 to 29. More importantly, Bergh mentioned the presence of a hermaphroditic gland independent from the digestive gland. This feature is exceptional in discodorids. It is also found in *Alloiodoris marmorata* Bergh, 1904, which is distinct from *coerulescens*. According to Bergh, the size of the receptaculum seminis (2 mm long) approximately equals that of the bursa copulatrix (1.5 mm in diameter). Finally, Bergh mentioned a 0.8 mm long penis.

DESCRIPTION OF NEW SPECIMENS (Figs. 258-273).— *Color*. The ground color of the dorsal notum of live animals is whitish-grayish and bears some irregular, darker blotches and spots. The number, size, and color (brown or black) of those spots vary among individuals. At higher magnification, some minute dark dots can be observed. A white continuous line runs along the margin of the dorsal notum. Sometimes, however, this line is not a full circle. A similar white line may be present on the margins of the branchial plumes too. The rhinophores are yellowish-light brown. The dorsal notum of preserved specimens is whitish (CASIZ 161292), creamish (CASIZ 074198, CASIZ 086325, CASIZ 105689), light pink (CASIZ 157476), creamish with light brown blotches and spots (MNHN, CASIZ 103713, CASIZ 071702), white with distinct black blotches and spots (CASIZ 070167). The ventral surface (hyponotum and foot) of preserved animal is whitish or creamish, without dots or spots.

External morphology. The body is oval. The length equals less than twice the width. The largest specimen is 25 mm long, preserved, i.e., about 35 mm alive. The foot is rounded posteriorly and anteriorly. The width of the foot equals about one third or one half of the width of the dorsal notum (in preserved specimens). The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, but not grooved. The dorsal notum bears tubercles that are not caryophyllidia. Well-preserved tubercles have a densely ciliated apex, as in caryophillidia, except that the protruding spicules are not arranged in a regular crown. Many small holes (diameter < 10 μm) and many tufts of cilia are present on the surface of the dorsal notum, including the rhinophores and the gills. In preserved specimens, the margins of the rhinophoral and branchial sheaths are smooth or crenulate. There are six tripinnate branchial plumes. The rhinophores have from 10 to 25 lamellae.

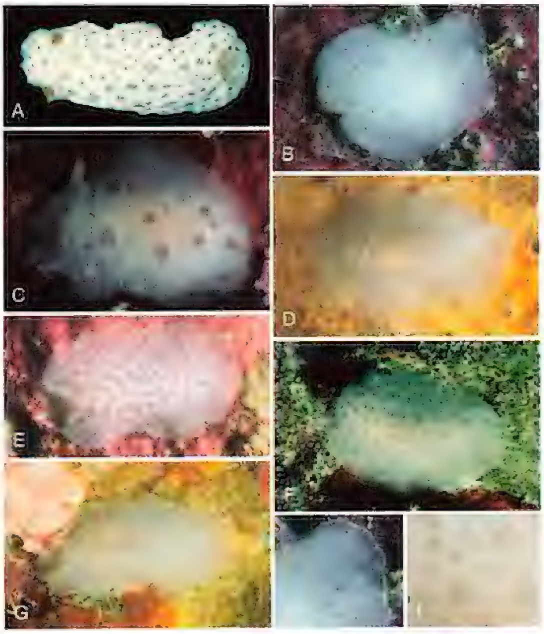

FIGURE 258. *Discodorididae coerulescens*, dorsal color. A. CASIZ 070167 (R.F. Bolland).— B. CASIZ 161292 (T.M. Gosliner).— C. CASIZ 105689 (T.M. Gosliner).— D. CASIZ 157476 (T. M. Gosliner).— E. CASIZ 103712 (T.M. Gosliner).— F. CASIZ 074198 (T. M. Gosliner).— G. CASIZ 086325 (T.M. Gosliner).— H. Mantle margin, CASIZ 161292 (T.M. Gosliner).— I. Dorsal spots and blotches, detail, CASIZ 157476 (T.M. Gosliner).

Digestive system. The digestive gland is dark orange in most preserved specimens, but not all. The stomach is large, free, on top of the left anterior side of the digestive gland. A small caecum is present. Exceptionally, the caecum is large (CASIZ 071702). The intestine is straight and dorsal. The labial cuticle is armed with a pair of jaw plates constituted by rodlets. The labial cuticle seems to be smooth in two specimens (MNHN #1, CASIZ 070167). The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. Radular formulae are: 12 × (22-0-22) in a 11 mm long specimen (CASIZ 161292), 15 × (29-0-29) in a 15 mm long specimen (CASIZ 105689), 15 × (31-0-31) in a 21 mm long specimen (CASIZ 103712), 18 × (34-0-34) in a 15 mm long specimen (CASIZ 086325), 17 × (32-0-32) in a 17 mm long specimen (CASIZ 157476), 20 × (36-0-36) in a 23 mm long specimen (CASIZ 074198), 19 × (44-0-44) in a 20 mm long specimen (CASIZ 070167), 19 × (44-0-44) in a 24 mm long specimen (MNHN #1), 17 × (29-0-29) in a 17 mm long specimen (CASIZ 157476), 22 × (27-0-27) in a 15 mm long specimen (MNHN #2), 21 × (44-0-44) in a 20 mm long specimen (CASIZ 071702), and 23 × (43-0-43) in a

25 mm long specimen (CASIZ 103713). The rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the teeth gradually increases towards the edges, up to three fourth of the row, and then gradually decreases; the two outermost teeth have a reduced base, and the last outermost tooth can be vestigial. The teeth are not grooved and bear no denticles. However, denticles were found on the last outermost tooth of the radula of three specimens (CASIZ 161292, CASIZ 074198, CASIZ 105689). In the smallest radula, the last three outermost teeth bear denticles (CASIZ 161292). Note that, in a single radula, not all rows have a last outermost tooth with denticles (e.g., CASIZ 105689).

Nervous system. The length of the circum-esophageal nerve ring equals up to three times the width of the dorsal ganglia. All ganglia are more or less fused. Their surface is smooth.

Reproductive system. The whitish hermaphroditic gland is independent from the digestive gland and is tightly attached to the rest of the reproductive system. The ampulla is convoluted (one to four tight loops). The division between male and female ducts could not be seen by dissection. The prostate is divided in a proximal whitish part and a distal yellowish-orange part. The deferent duct is short. It is straight or convoluted with a few loose loops in its distal part. In the smallest (< 2 mm in length) reproductive system, the deferent duct was convoluted from the prostate up to the penial sheath (CASIZ 161292). A penial papilla is present in the distal part of the deferent duct, but not in all specimens. The fact that no distinct, copulatory organ was found in several specimens (CASIZ 078198, CASIZ 086325, CASIZ 105689) suggests that this papilla corresponds to the evaginable distal part of the deferent duct, rather than a permanent, distinct penis. Papillae are flattened and more or less rectangular, or cylinder-like and elongated. Papilla shapes certainly vary due to different papilla retraction stages at fixation. They meas-

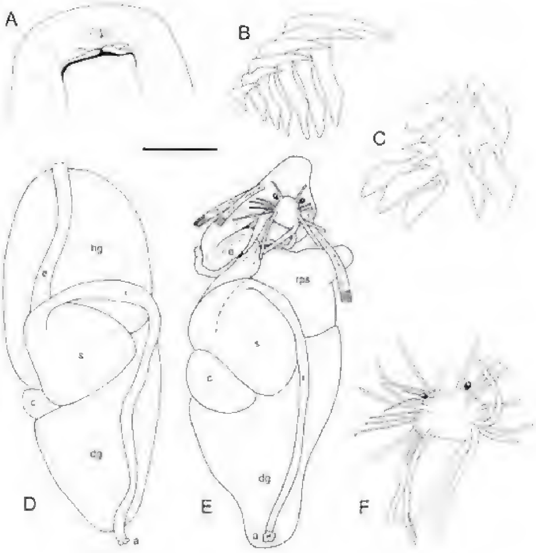

FIGURE 259. *Discodorididae coerulescens*. A. Anterior, ventral view, CASIZ 074198, scale = 2.5 mm.— B. Outermost radular teeth, after Bergh (1888: plate LXXXIII, fig. 9).— C. Innermost radular teeth, after Bergh (1888: plate LXXXIII, fig. 7).— D. Internal anatomy, buccal mass removed, CASIZ 073713, scale = 3.5 mm.— E. Internal anatomy, CASIZ 071702, scale = 3 mm.— F. Nervous system, CASIZ 071702, scale = 1.5 mm.

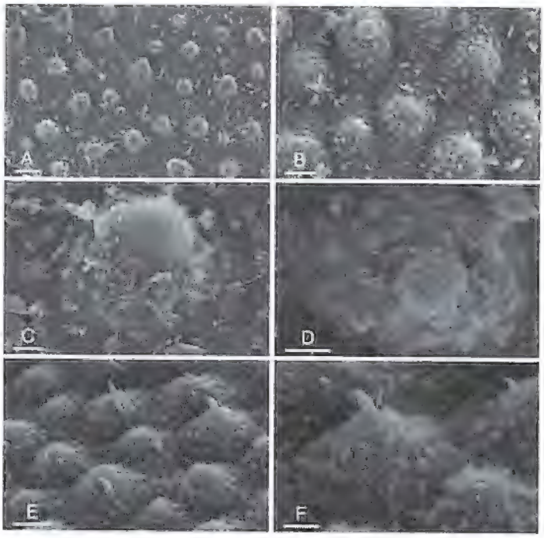

FIGURE 260. *Discodorididae coerulescens*, notum. A. Tubercles, CASIZ 103712, scale = 100 µm.— B. Tubercles, CASIZ 103712, scale = 60 µm.— C. Tubercle, CASIZ 103712, scale = 20 µm.— D. Tubercle, CASIZ 103712, scale = 30 µm.— E. Tubercles, CASIZ 086325, scale = 60 µm.— F. Tubercle, CASIZ 086325, scale = 30 µm.

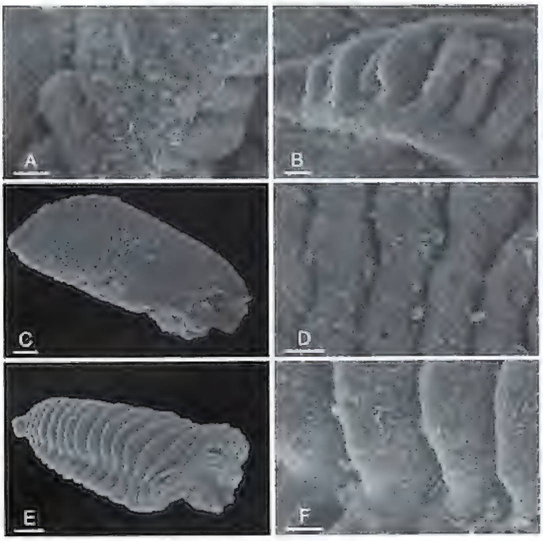

FIGURE 261. *Discodorididae coerulescens*. A. Branchial plume, detail, CASIZ 086325, scale = 40 µm.— B. Branchial plume, detail, CASIZ 103713, scale = 40 µm.— C. Rhinophore, CASIZ 103713, scale = 200 µm.— D. Rhinophoral lamellae, CASIZ 103713, scale = 40 µm.— E. Rhinophore, MNHN (#1), scale = 200 µm.— F. Rhinophoral lamellae, MNHN (#1), scale = 40 µm.

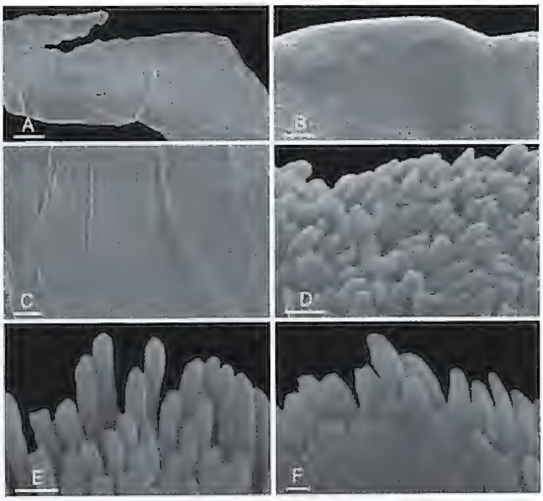

FIGURE 262. *Discodorididae coerulescens*, labial cuticle. A. Smooth labial cuticle, MNHN (#1), scale = 200 µm.— B. Smooth labial cuticle, detail, MNHN (#1), scale = 20 µm.— C. Smooth labial cuticle, detail, CASIZ 070167, scale = 40 µm.— D. Jaw rodlets, CASIZ 103713, scale = 10 µm.— E. Jaw rodlets, CASIZ 074198, scale = 10 µm.— F. Jaw rodlets, CASIZ 161292, scale = 4 µm.

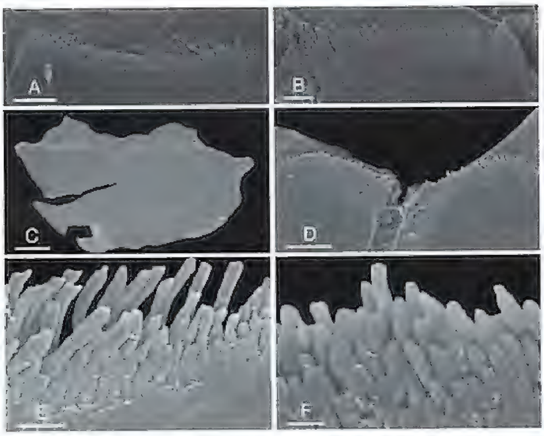

FIGURE 263. *Discodorididae coerulescens*, labial cuticle. A. One lateral jaw plate, CASIZ 103712, scale = 60 µm.— B. One lateral jaw plate, CASIZ 086325, scale = 40 µm.— C. Pair of jaw plates, CASIZ 071702, scale = 200 µm.— D. Pair of jaw plates, CASIZ 105689, scale = 200 µm.— E. Jaw rodlets, CASIZ 071702, scale = 20 µm.— F. Jaw rodlets, CASIZ 105689, scale = 10 µm.

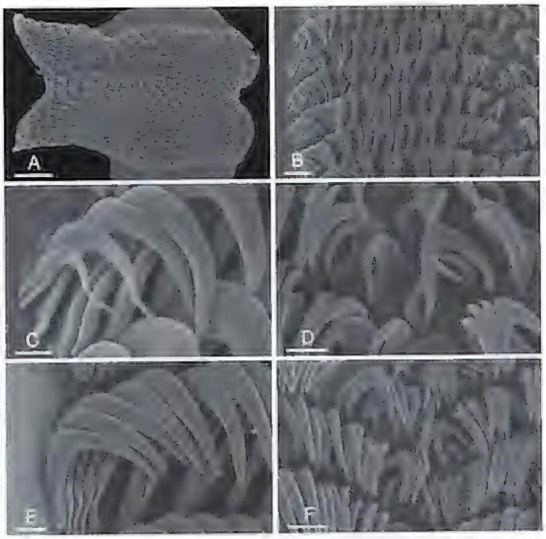

FIGURE 264. *Discodorididae coerulescens*, radula. A. MNHN (#2), scale = 200 µm.— B. Left rows, MNHN (#2), scale = 40 µm.— C. Outermost teeth, MNHN (#2), scale = 10 µm.— D. Innermost teeth, MNHN (#2), scale = 20 µm.— E. Outermost teeth, CASIZ 070167, scale = 20 µm.— F. Innermost teeth, CASIZ 070167, scale = 40 µm.

ure from 0.2 to 0.5 mm in length. The papillae of the two largest specimens (MNHN #1, CASIZ 103713) have a crown of small, soft conical hooks around the apex, even though they are not significantly larger than the other papillae (respectively 0.55/0.2 mm and 0.3/0.18 mm). The other papillae are smooth, with the usual cilia found on the surface of most discodorid papillae. The vagi-

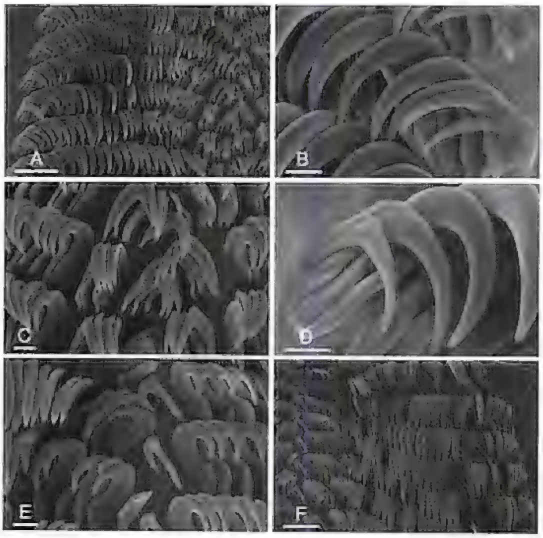

FIGURE 265. *Discodorididae coerulescens*, radula. A. Left rows, CASIZ 074198, scale = 100 µm.— B. Outermost teeth, CASIZ 074198, scale = 20 µm.— C. Innermost teeth, CASIZ 074198, scale = 20 µm.— D. Outermost teeth, CASIZ 157476, scale = 20 µm.— E. Innermost teeth, CASIZ 086325, scale = 20 µm.— F. Right rows, CASIZ 086325, scale = 100 µm.

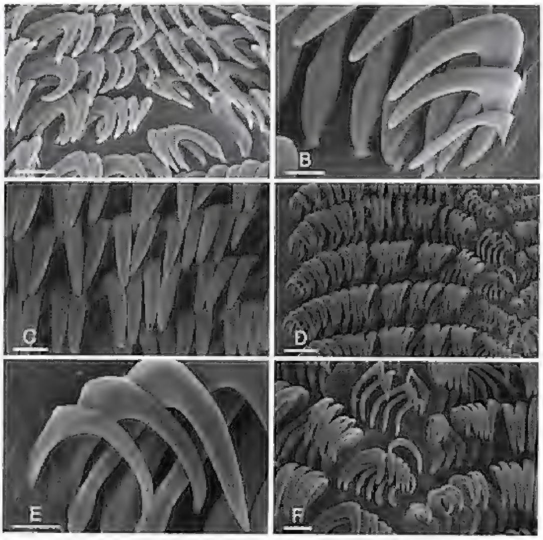

FIGURE 267. *Discodorididae coerulescens*, radula. A. Innermost teeth, CASIZ 103713, scale = 40 µm.— B. Outermost teeth, CASIZ 103713, scale = 20 µm.— C. Median teeth, CASIZ 103713, scale = 40 µm.— D. Left rows, CASIZ 103712, scale = 100 µm.— E. Outermost teeth, CASIZ 103712, scale = 20 µm.— F. Innermost teeth, CASIZ 103712, scale = 40 µm.

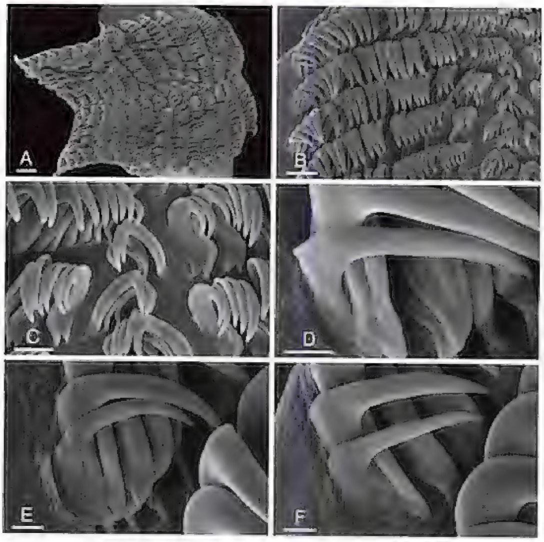

FIGURE 266. *Discodorididae coerulescens*, radula, CASIZ 105689. A. Scale = 100 µm.— B. Left rows, scale = 60 µm.— C. Innermost teeth, scale = 30 µm.— D. Outermost teeth, scale = 10 µm.— E. Outermost teeth, scale = 10 µm.— F. Outermost teeth, scale = 10 µm.

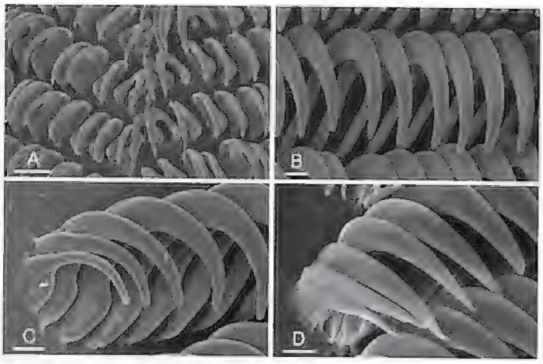

FIGURE 268. *Discodorididae coerulescens*, radula. A. Innermost teeth, CASIZ 071702, scale = 50 µm.— B. Median teeth, CASIZ 071702, scale = 20 µm.— C. Outermost teeth, CASIZ 071702, scale = 20 µm.— D. Outermost teeth, CASIZ 161292, scale = 10 µm.

nal duct is straight or loosely convoluted. The vaginal duct of the smallest reproductive system (CASIZ 161292) is more convoluted. The fertilization duct is short, straight or loosely convoluted. The disappearance of the fertilization duct into the female gland mass is marked by a distinct duct. The duct of the receptaculum seminis is short but distinct. The bursa copulatrix is slightly larger than the receptaculum seminis. An empty bursa copulatrix can be smaller than the receptaculum seminis (CASIZ 157476). Both pouches are spherical-ovate and smooth.

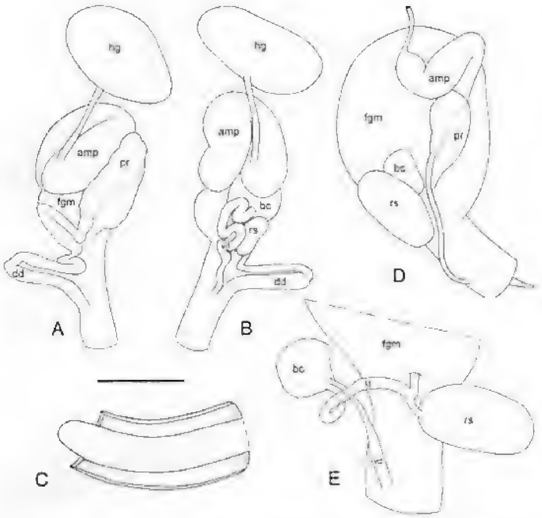

FIGURE 269. *Discodorididae coerulescens*, reproductive system. A. CASIZ 161292, scale = 0.5 mm.— B. CASIZ 161292, scale = 0.5 mm.— C. Penial papilla in penial sheath, CASIZ 161292, total length = 0.2 mm.— D. Hermaphroditic gland not represented, CASIZ 157476, scale = 1.5 mm.— E. Spermatic pouches, CASIZ 157476, scale = 1.3 mm.

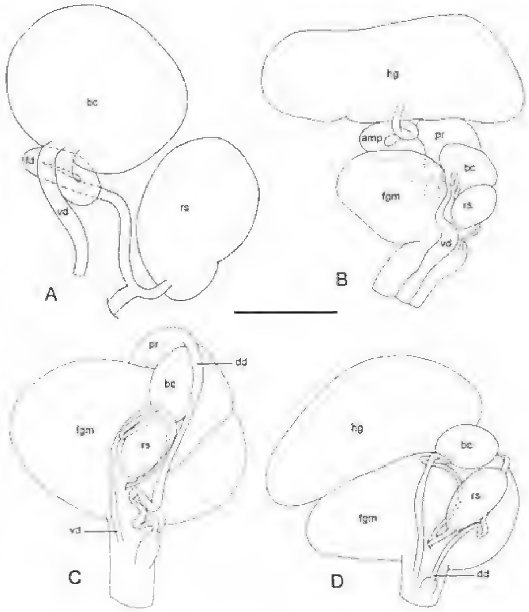

FIGURE 271. *Discodorididae coerulescens*, reproductive system. A. Spermatic pouches, MNHN (#1), scale = 1 mm.— B. MNHN (#1), scale = 3.2 mm.— C. Hermaphroditic gland not represented, CASIZ 103713, scale = 2.5 mm.— D. CASIZ 074198, scale = 1.3 mm.

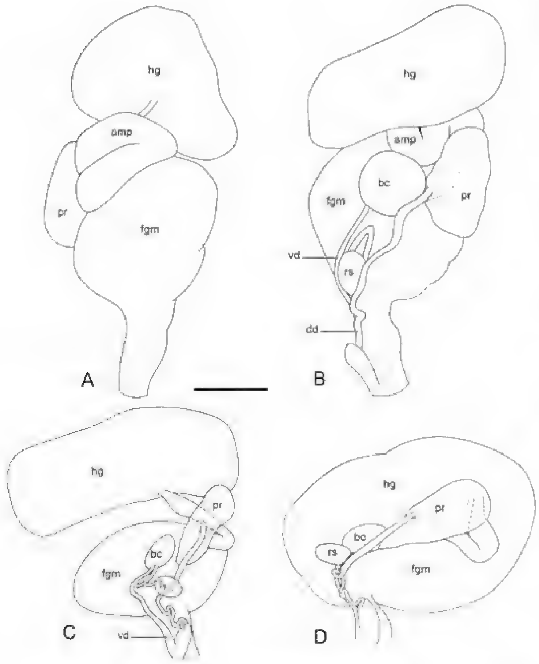

FIGURE 270. *Discodorididae coerulescens*, reproductive system. A. CASIZ 105689, scale = 0.7 mm.— B. CASIZ 105689, scale = 0.5 mm.— C. CASIZ 071702, scale = 0.8 mm.— D. CASIZ 071702, scale = 1.5 mm.

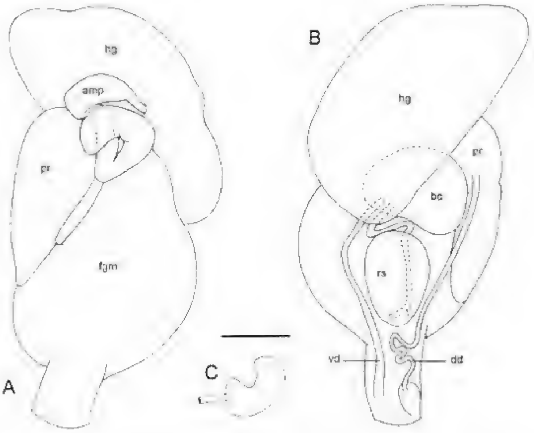

FIGURE 272. *Discodorididae coerulescens*, reproductive system. A. CASIZ 070167, scale = 1 mm.— B. CASIZ 070167, scale = 1 mm.— C. Papillae, CASIZ 070167, scale = 0.3 mm.

Diagnostic features.— The color of the dorsal notum of live animals is a good diagnostic feature of *coerulescens*. It could potentially be confused with the dorsal color of *murrea*. However, the pictures of live animals presented here should help people distinguish these two species: *murrea* does not have a continuous white line along the margin of the notum, and that its marble-like pattern is quite different from the blotches and spots found in *coerulescens*. In any case, the independent hermaphroditic gland and the general organization of the reproductive system should help identify both live and preserved specimens without difficulty.

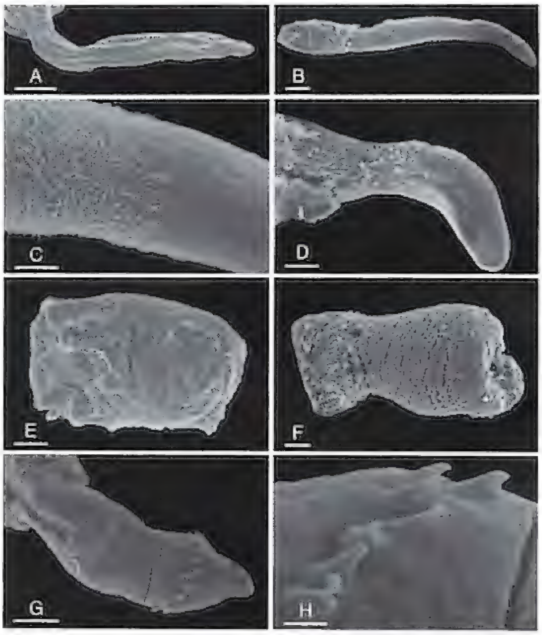

Figure 273. *Discodorididae coerulescens*, penis. A. CASIZ 157476, scale = 100 µm.— B. CASIZ 105689, scale = 60 µm.— C. CASIZ 105689, scale = 20 µm.— D. MNHN (#2), scale = 40 µm.— E. CASIZ 071702, scale = 40 µm.— F. CASIZ 103713, scale = 40 µm.— G. MNHN (#1), scale = 100 µm.— F. MNHN #1, scale = 20 µm.

Infra-specific character variation.— Anatomical and morphological data available in the literature (Bergh 1888; Edmunds 1971) are compatible with the description provided here, but Bergh observed from 40 to 50 rhinophoral lamellae. The largest animals known are 30 mm long, alive (Edmunds 1971) and 28 mm long, preserved (Bergh 1888). The radular formulae given by Bergh —25/29 × (45-0-45)— and Edmunds —21 × (37-0-37)— are compatible with the individual variation observed here: the number of rows ranges from 12 (for 22 teeth per half row) up to 23 (for 43 teeth per half row); the maximum number of teeth per half row ranges from 22 (for 12 rows) to 44 (for 19 and 21 rows). The reproductive system illustrated by Edmunds also is compatible with observations provided here, in particular the relative size of spermatic pouches and the length of the different ducts. The length of the penial papilla, when present varies from 0.2 to 0.8 mm long (Bergh 1888; present study).

Discussion.— Bergh did not compare *coerulescens* with any other species. Edmunds (1971) thought that *coerulescens* was similar to *Discodoris labifera*. The color of live animals of *labifera* is unknown, but its internal anatomy is distinct from the anatomy of *coerulescens*: *Discodorididae labifera* has a hermaphroditic gland that is not independent from the digestive gland and a strong penis. Edmunds (1971) also argued that a better knowledge of the infra-specific variation of several features (e.g., absence/presence of jaws, color pattern, dorsal tubercles) could lead us to accept a synonymy between *coerulescens* and *mauritiana* (i.e., *Peltodoris murrea*). Actually, *Discodorididae coerulescens* and *Peltodoris murrea* are perfectly distinct. However, Edmunds (1971:351) rightly pointed out that the presence/absence of rodlets is a "very trivial character on which to separate two genera especially when we do not know how constant it is in a wide variety of specimens, nor whether it is absent in young animals and only developed as they mature."

Several differences among individuals are regarded here as infra-specific variations, such as the presence/absence of soft conical hooks on the penial papilla and the presence/absence of denticles on the outermost lateral tooth. The hypothesis that these differences are inter-specific must be rejected because, for example, the two specimens #1 and #2 collected from the same locality in New Caledonia are hardly distinguishable except for their penial papillae, and, more importantly, the presence/absence of denticles on the last outermost tooth varies among rows within a single radula (the denticle is found in some rows, not in all).

Supra-specific relationships.— A phylogenetic test of the relationships of *coerulescens* shows that *coerulescens* does not belong to *Discodoris*. It is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial for *coerulescens* should be *"Montereina" coerulescens*. Possible names under the *ICPN* are *"Montereina" coerulescens* or simply *Discodorididae coerulescens*.

Future studies.— Some individual variations, especially for the penial papilla, suggest that *coerulescens* could actually include cryptic species. This matter will likely need to be investigated with non-morphological data as well.

"*Montereina*" *concinna* (Alder and Hancock, 1864) New combination
***Discodorididae concinna* (Alder and Hancock, 1864) New combination**

Doris concinna Alder and Hancock, 1864:118, plate XXVIII, figs 4-6.
Discodoris concinna.— Bergh, 1877a:519.

Type material.— The type material could not be found. It is not at the Hancock Museum, Newcastle-upon-Tyne. Eliot (1906b, c) commented on the collection made by Walter Elliott, from southern India, which was used by Alder and Hancock to describe several new species, including *concinna*. Given that the type material of *concinna* could not be found at the Hancock Museum, Eliot's (1906b:651) notes are essential: "Four specimens labeled in Hancock's writing «Nos. 14, 23, 85, 115. *Doris concinna*. Madras. Mr. W. Elliott.» There is also a note to the effect that the specimens were found partly dried up in 1902. They are now in spirit; but their hard and stiff texture is probably the result of their desiccation." Eliot (1906c) also found one (or two) slide(s) with a labial armature and the radula. This (or these) slide(s) could not be found either.

Type locality.— Madras, eastern India (according to Eliot's notes on the type material). According to the original description, Walter Elliot collected the specimens from Vizagapatam, i.e., Vishakhapatnam, also is in eastern India, but distinct from Madras.

Remarks on the original description.— Alder and Hancock's (1864:118) brief description is reproduced here in its entirety. "Body oval, rather convex, brownish. Cloak with smallish, conical, finely pointed tubercles, rather soft and much attenuated towards the margin, placed a little apart with small ones interspersed; it is yellowish or reddish brown, sometimes inclined to grey, with large dark blotches (often rather obscure) on the sides of the back, and spotted with brown over the whole surface. Under side pale yellowish brown, irregularly spotted with dark brown, and minutely reticulated with white. Dorsal tentacles clavate, brown. Oral tentacles pointed. Branchial plumes six, quadripinnate, yellowish brown, with darker brown freckles; the margin of the cavity slightly raised. Foot broad, grooved and notched in front, of a yellowish or reddish brown, freckled with a darker shade of the same colour; the upper surface paler, with dark brown spots. Length from 21/2 to 3 inches. The young is paler and more minutely spotted. Spicula small, pointed, a little bent, arranged in a reticulated manner, and in bundles at the base of the tubercles. The tongue is similar to that of *D. tuberculata*; but the mouth is also supplied with a prehensile collar. The spawn is riband-formed, with the free margin sinuous, forming one or two irregular coils. This is a common species." Eliot's (1906b:651-652) notes also are reproduced here: "So far as one can judge from such old material, Alder and Hancock's description and plate are quite accurate. The colour of the under side and the foot appears to be variable, being in some specimens pale and spotted, in others darker and livid (*cf.* the varieties of *D. concinniformis* Bergh). The shape and elevation of the branchial opening are also variable. In one specimen it is nearly closed; in another it is almost stellate. But in its natural condition it seems to be broad and circular. The foot is broad, grooved, and notched in front. The oral tentacles are long, digitate, and pointed. The most distinct external character is that the back is studded with small tubercles of varying size and of lighter tint than the ground-color. The peculiar effect which this produces in the appearance of the animal is well rendered in Alder and Hancock's plate. The tubercles are of somewhat irregular outline, and often have a long pointed tip. Though they are numerous, they are separated from one another by distinct intervals. Though the tissues of the buccal organs are decayed, the hard parts are still recognizable. The labial armature is formed of longish, bent, transversely striated rods. The teeth are yellowish, hamate, moderately stout, and of a somewhat wavy outline. They are like Bergh's plates in the 'Siboga' Expedition (pl. xiv, fig. 4). The genitalia are decayed, but no armature was found. Bergh in describing various specimens of his *Discodoris concinniformis*, has indicated its probable identity with this species. There is no divergence in the buccal parts; but it is curious that Bergh, while describing *D. concinniformis* as bearing light-coloured spots, does not state definitely that the tubercles are lighter that the dorsal surface, which is the cause of the peculiar colouration of *D. concinna*." Eliot (1906c:1005) then added some comments on the radula and the labial cuticle: "Labial armature composed of two triangular plates, consisting of a dense mass of irregular and sinuous rods. The radula consists of 17 complete rows and fragments of 3 or 4 others, with 45 teeth on either side of the rachis in the longest rows. The innermost teeth are markedly lower than the rest and project into the wide rachis: the outermost are smaller but not degraded.

DISCUSSION.— My intuition about the original description of *concinna* is that it was based on young specimens or light variants of *Sebadoris fragilis*, which is supported by the length of the specimens (from 63 to 76 mm) and the dorsal color. However, the original description of *concinna* and Eliot's notes on the type material are ambiguous for several reasons. Large and dark specimens of *Sebadoris fragilis* may be identified (though not with certainty) owing to some general features (e.g., black ring on the hyponotum adjacent to the foot, length up to 150 mm, more than 40 teeth per half row). However, when specimens of *Sebadoris fragilis* are smaller and with a lighter dorsal color, their general appearance can be easily confused with several other species of discodorids with brown blotches on the dorsal notum, especially *Tayuva lilacina*. The length (from 63 to 76 mm) is problematic because the longest specimen of *lilacina* found measured 58 mm long (at least in the Indo-West Pacific), which is close to 63 mm. Finally, the radular formula of 21 × (45-0-45) is problematic because the maximum number of teeth per half row that I found in *lilacina* was 40 (at least in the Indo-West Pacific), which is not too distant from 45 teeth. The pigmentation of both the hyponotum and the foot is compatible with both *Tayuva lilacina* and *Sebadoris fragilis*. Eliot insisted on the fact that the distinct feature of *concinna* was the presence of tubercles with a lighter tint than the dark background. A similar pattern was found in several preserved specimens of *fragilis*, and Willan and Coleman (1984) and Wells and Bryce (1993) published color pictures of this pattern for specimens that they identified as *concinna* but that should be part of *fragilis*. However, note that the tubercles of *lilacina* also are lighter than the dorsal background.

Here *concinna* is regarded as as a *nomen dubium* rather than a synonym of *fragilis*. The main reason is that, although several features suggest that specimens described as *concinna* by Alder and Hancock were young *Sebadoris fragilis* (size, radular formula, etc.), one cannot exclude that they were large *Tayuva lilacina*. There are two other important reasons why regarding *concinna* as a *nomen dubium* is appropriate. First, it cannot be excluded that the syntypes of *concinna* were part of different species (e.g., *lilacina* and *fragilis*) instead of just one species. Also, the dorsal color described by Alder and Hancock is potentially compatible with other discodorid species, such as *Discodorididae labifera*, which looks externally like *lilacina* or a young, pale *fragilis* specimen.

Because of the ambiguity of the original description of *concinna*, specimens identified as *concinna* in the literature are not part of a single species. Most specimens identified as *concinna* are ambiguous. Many specimens identified as *concinna* probably were part of *Sebadoris fragilis*, with more or less confidence (Eliot 1909a, 1913; Vayssière 1912; Baba 1933, 1949; Gohar and Soliman 1967; Lim and Chou 1970; Thompson 1975; Willan and Coleman 1984; Guangyu 1986; Coleman 1989; Wells and Bryce 1993; Dayrat and Gosliner 2005). The identification of those specimens is commented on in the discussion of *Sebadoris fragilis*.

Here several other specimens are added. The 42 mm long specimen identified as *concinna* by Eliot (1906a) from Minikoi, Laccadive Sea, could be part of several species, such as *Sebadoris fragilis*, *Tayuva lilacina*, and *Discodorididae labifera*. The three specimens (maximum 41 mm long) identified as *concinna* by Eliot (1913) from Kominato, Awa, Japan, could be part of several species too. Their radular formulae of 20 × (40-0-40) and 24 × (40-0-40) do not allow us to exclude any identification. Note that Kominato is in Tokyo Bay, almost at 36°N, and this specimen may not be part of a tropical species, such as *Sebadoris fragilis* and *Tayuva lilacina*. In Japan, a specimen was found to be similar to *fragilis* externally but with a completely different penis (CASIZ 082038). This suggests that other species that could be confused with *Sebadoris fragilis* are present in Japanese waters. Until we know more about those species, it will remain difficult to identify species just based on a picture of the dorsal notum. The black-and-white drawing for a specimen of *concinna* from Toyama Bay, by Abe (1964:52-53, plate 24, fig. 87) can hardly be used here because it is not precise. The picture of the *concinna* specimens by Okutani (2000) may illustrate a *Sebadoris fragilis* specimen. However, Okutani records *concinna* from Boso Peninsula (35°N) as well as Sado Island (38°N), which would be a northern limit. As a result, it is difficult to identify the specimen from Izu Peninsula, Japan (35°N), identified as *concinna* by Suzuki (2000). It could be *fragilis* or some other *fragilis*-like species. The 20 mm long specimen from the Gulf of Aqaba, Red Sea, identified as *concinna* by Engel and Eeken (1962) probably were part of *Tayuva lilacina*, although it is difficult todetermine what the authors actually observed. Finally, note that several authors have mentioned the name *concinna* in checklists of *Discodoris* species names, without adding new material or data (Bergh 1877a, 1884a; Eliot 1910a; O'Donoghue 1929; Risbec 1956; Zhongguo 2001).

Several authors (e.g., Barash and Danin 1977, 1982, 1987; Costello et al. 2001) have mentioned the presence of *concinna* in eastern Mediterranean, supposedly as a so-called Lessepsian migrant (i.e., a species that migrated from the Red Sea to the Mediterranean through the Suez Canal). In the present study, specimens identified as *concinna* from eastern Mediterranean are thought to be part of *Tayuva lilacina*, which includes its synonym *Tayuva maculosa*, the native Mediterranean species overlooked by those authors.

Finally, two pictures of specimens identified as *concinna* were found on the *www*. A 30 mm long specimen, from Kii Peninsula, Japan, most likely is part of *Tayuva lilacina*. A 65 mm long specimen, from Abugashima, Toyama Bay, could be part of *Sebadoris fragilis*.

Several authors (e.g., Edmunds 1971, 1972; Rao and Kumary 1974; Thompson 1975; Soliman 1983) have attempted to distinguish *concinna* from *fragilis*. However, all those attempts have failed (see *Sebadoris fragilis*). First, the vague original description of *concinna* led people to identify organisms of distinct species as *concinna*. Second, authors have used the literature as a fundamental source of data and taken all identifications for granted. As a result, authors were unable to distinguish two entities because those were a mix of a little bit of everything, and certainly not two homogeneous entities. For example, everybody has accepted Kay and Young's (1969) specimens of *fragilis* from Hawaii as '*fragilis*,' although they clearly are part of *lilacina*. Naturally, authors (e.g., Edmunds 1971, 1972) have had a hard time explaining why the radular formulae found by Kay and Young were much smaller than in the rest of *fragilis*.

Several authors (Eliot 1906b, c, 1909a, 1910a, 1913; O'Donoghue 1929; Edmunds 1971, 1972; Thompson 1975) have regarded *concinniformis* as a synonym of *concinna*. It is already hard to know what *concinna* is, and it is even harder to decide whether or not *concinniformis* is a synonym of *concinna*.

Supra-specific relationships.— A phylogenetic test of the relationships of *concinna* shows that *concinna* does not belong to *Discodoris*. It is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial for *concinna* should be *"Montereina" concinna*. Possible names under the *ICPN* are *"Montereina" concinna* or simply *Discodorididae concinna*. The unknown position of *concinna* is largely due to the fact that the necessary data to solve its position are lacking from the original description.

"Montereina" concinniformis (Bergh, 1888) New combination
Discodorididae concinniformis (Bergh, 1888) New combination

Discodoris concinniformis Bergh, 1888:807-809, plate LXXXIII, figs 1-5.— Bergh, 1890:900-902.— Bergh, 1905:100-102, plate XIV, figs 3-5.

Type material.— Holotype (ZMB 43945), by monotypy: one specimen 45/30 mm preserved length.

Type locality.— Ile aux Fouquets [not Phuket, Thailand, see Jensen, 1998], Mauritius, Indian Ocean. The label of the holotype simply indicates Mauritius.

Distribution.— Mauritius (type locality), Amboina, i.e., Ambon, Indonesia (Bergh 1890), and northwestern end of Timor (Bergh 1905).

Type material condition.— The specimen was dissected by Bergh and only the external body wall (entirely white) remains in the jar.

Remarks on the original description (*concinniformis*).— The original description of *concinniformis* is globally uninformative because most characters are general and compatible with many discodorid species. As usual, Bergh does not mention any feature that could help us identify *concinniformis*. The specimen measured 50/32 mm. The dorsal color is dirty yellowish with brownish-grey and blackish spots. The indication that spots are "generally not small, occasionally large" is ambiguous. The undersurface is dirty yellowish with large and small purple-grey spots. The rhinophores are olive-brownish with a white tip, and the six branchial plumes are olive-brownish too. The dorsal notum is covered with hemispherical tubercles. The rhinophores have from 60 to 70 lamellae. The number of lamellae is high, but Bergh occasionally gave unexpectedly high numbers of lamellae (e.g., see *Discodorididae coerulescens* and *Sebadoris fragilis*). Bergh mentioned two jaw plates, and a radular formula of 31 × (55-0-55). The outermost teeth, illustrated by Bergh, are hamate (not vestigial), which by no means is diagnostic of a particular species. In the reproductive system, Bergh described a 2.5 mm long "invaginated" penis, and indicated that it was "as usual," which may mean that it was a simple papilla, lacking humps or hooks. The rest of the description of the reproductive system (e.g., sac-shaped, 3 mm long bursa copulatrix, and sausage-shaped, 2 mm long receptaculum) is general. The absence of illustration makes it difficult to use.

Discussion.— Bergh (1888, 1905) repeated that *concinniformis* could actually be *concinna*. Bergh's description surely is compatible with the original description of *concinna*. However, any vague description can be compatible with another vague description, and the original descriptions of *concinna* and *concinniformis* are unquestionably vague. The question of the application of *concinniformis* is as open as the question of the application of *concinna*. There is a chance that Bergh identified as *concinniformis* some variants of *Sebadoris fragilis* (although the number rhinophoral lamellae is problematic), but other possibilities cannot be excluded. Several authors have regarded *concinniformis* as a synonym of *concinna* (e.g., Eliot 1906b, c, 1909a, 1910a, 1913; O'Donoghue 1929; Edmunds 1971, 1972; Thompson 1975). The examination of the type material does not help: the holotype of concinniformis could be a young *fragilis*, but it could be part of other species as well, such as *Tayuva lilacina*. Thus, *concinniformis* is regarded here as a *nomen dubium*.

Bergh described three additional specimens of *concinniformis*: two from Ambon (Bergh 1890) and one from the northwestern end of Timor (Bergh 1905). Could we re-identify these specimens, despite the fact that *concinniformis* is a *nomen dubium*? Two of those specimens do not seem to be part of *Tayuva lilacina*, because the radular formulae seem to be incompatible with the variation observed for *lilacina* (maximum of 40 teeth per half row in a 58 mm long specimen): one 45 mm long specimen from Ambon had a radular formula of 27 × (44-0-44), and the 35 mm long specimen from Timor had a radular formula of 40 × (58-0-58). The 28 mm long specimen from Ambon has a radular formula of 24 × (37-0-37), which is not incompatible with *lilacina*. Note that Bergh identified the specimens from Ambon as *concinniformis* although he counted only 25 and 30 rhinophoral lamellae (Bergh did not mention the number of lamellae in the specimen from Timor). This difference in the number of rhinophoral lamellae and some other differences (e.g., the dark blue hyponotum of the variety of *concinniformis*, and the radular formulae of the two specimens from Ambon) suggest that Bergh may have used a single name for specimens that were part of more than one species. This would not be the first time (see, e.g., *Discodorididae notha* and *Discodorididae crucis*). In fact, Bergh (1888:809-811) also described a variety of *concinniformis*. The material of that variety was examined for the present study: it clearly is part of *Sebadoris fragilis* (see that species).

Supra-specific relationships.— A phylogenetic test of the relationships of *concinniformis* shows that *concinniformis* does not belong to *Discodoris*. It is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial for *concinniformis* should be *"Montereina" concinniformis*. Possible names under the *ICPN* are *"Montereina" concinniformis* or simply *Discodorididae concinniformis*.

"*Montereina*" *crucis* (Ørsted *in* Mörch, 1863) New combination
Discodorididae crucis (Ørsted *in* Mörch, 1863) New combination

Figure 274.

Doris (*Dendrodoris*) *crucis* Ørsted *in* Mörch, 1863:33-34.
Discodoris crucis.— Bergh, 1877a:519.— Bergh, 1878a: xxv.— Bergh, 1879b: plate V, figs 3-8.
Peltodoris crucis.— Bergh, 1880a:41-46, plate A, figs 1-2.— Rochebrune, 1881:263.

Type material.— One lectotype (ZMUC, no catalogue number), designated here: one specimen 53/30 (#1) mm preserved [just the body wall, without the edges of the notum], leg. Riise, 23 June 1858. Three paralectotypes (ZMUC, no catalogue number), designated here: one specimen 53/35 (#2) mm preserved [just the body wall, without the margins of the dorsal notum], leg. Riise, 23 June 1858; two specimens 53/25 (#3) and 60/35 (#4) mm preserved, leg. Riise, [no collecting date]. Prior to the present study, the type material would include four syntypes (ZMUC, no catalogue number), which are referred to as specimens #1, #2, #3, and #4. In a first jar, two specimens (#1 and #2) were identified as *Doris crucis* Ørsted. In a second jar, two specimens (#3 and #4) were identified as *Peltodoris crucis* Ørsted, although the name *Doris crucis* could hardly be read on an older label. All specimens were collected from St. Thomas by Riise. According to the original description, *crucis* was known from two of the Virgin Islands, St. Thomas (specimens collected by Riise), and St. Croix (specimens collected by Ørsted). However, the type material does not currently include any specimens collected from St. Croix by Ørsted. Therefore, the type material of *cru-*

cis currently held bythe ZMUC does not include all the original type material. Also, Bergh, who redescribed *crucis* seventeen years after Mörch's contribution, dissected two specimens from St. Thomas. The specimens dissected by Bergh probably were the two specimens #1 and #2, dissected prior to the present study. At least one specimen was partly dissected for the original description (Mörch indicated that the radula was large and with hamate teeth). This specimen could be one the two specimens re-dissected by Bergh, or a specimen collected from St. Croix by Ørsted.

The reason why a lectotype is designated in the present study is that the specimen #3 is part of *branneri* and the specimen #4 is part of *Tayuva lilacina*. Of course, this is compatible with the vague, largely uninformative original description. However, the anatomy of specimen #3 is not compatible with Bergh's re-description of *crucis*. If the specimen #3 had been selected as the lectotype, *Discodorididae branneri* would have become a synonym of *Discodorididae crucis*. This solution is rejected here because: 1) the original description is largely uninformative and does not include any indication of the diagnostic characters of *branneri*; and 2) Bergh's re-description of some type specimens of *crucis* would also be different from *branneri*. Therefore, it was decided to select one of the two specimens that had been dissected prior to the present study —most likely by Bergh— as the lectotype (specimen #1). Consequently, the fact that one type (specimen #3) is part of *branneri* and another type (specimen #4) is part of *lilacina* is not an issue. The paralectotypes (specimens #2, #3, and #4) are still part of the type material of *crucis*: only the lectotype (specimen #1) is the name-bearer; paralectotypes can be part of any other species.

TYPE LOCALITY.— The type locality is the locality of the lectotype designated here: St. Thomas, [Virgin Islands]. The paralectotypes also are from the type locality. Note that the original description also mentioned specimens from St Croix, Virgin Islands.

DISTRIBUTION.— Virgin Islands, Caribbean Sea.

TYPE MATERIAL CONDITION.— Two specimens (#1 and #2) were dissected prior to the present study, most likely by Bergh, who redescribed *crucis*. Several pieces of organs were found in the same jar: two body walls without the lateral notum (one body wall still possesses six branchial plumes); seven pieces of notum; pieces of digestive glands (probably two); one stomach and one intestine; six branchial plumes (including one destroyed). Although some pieces of notum clearly belong to the two body walls found in the jar, some other pieces of notum probably belong to other specimens not found in the jar. A piece of a radula found at the bottom of the jar was mounted on a SEM stub. In a separate tube, inside the jar, were also found: pieces of buccal masses (probably two) including salivary glands; one heart; one rhinophore (with about 25 lamellae); two destroyed reproductive systems (only the ampulla and the female gland mass); one pouch (hypothetically a receptaculum seminis). Because all pieces were mixed, it is impossible to distinguish the organs that belong to the lectotype (specimen #1) from the organs that belong to the paralectotype (specimen #2). The two other specimens (#3 and #4) were entire, and well preserved externally. Both were dissected for the present study: the specimen #3 is part of *Discodorididae branneri* (see this species), and the specimen #4 is part of *Tayuva lilacina* (see this species: Caribbean).

REMARKS ON THE ORIGINAL DESCRIPTION (Fig. 274).— The original description of *crucis* includes a brief morphological description in Latin and a brief discussion in French. It is unclear whether the description was written by Mörch, Ørsted, or both of them. Also, it is not possible to know if Ørsted created a new species name based only on the specimens that he collected or based on all specimens (his specimens from St. Croix and Riise's specimens from St. Thomas). This has some importance because Ørsted's specimens could not be found, and are probably lost. Ørsted may or may not have seen all specimens. Mörch may or may not have seen all specimens either. However, we have to consider that the author(s) of the original description intended to describe the totality of the material cited. The fact that part of this material is probably lost and the fact that specimens are part of at least two entities (see below) imply that the original description should be interpreted with much caution.

The original description provides information about the color: dorsal and ventral surfaces bearing small and large dark spots. Bergh (1880a: plate A, figs 1-2) published two black-and-white drawings of the color of both the ventral and the dorsal surfaces, based on Ørsted's originals. These drawings are unrealistic, schematic illustrations of a color pattern commonly found in discodorids: whitish ground color bearing dark patches and dots. In the Caribbean Province, at least two species (*Tayuva lilacina* and *Discodorididae branneri*) have this dorsal color pattern. This certainly explains why two paralectotypes of *crucis* (specimen #3 and #4) are actually part of *branneri* and *lilacina*. Also, Bergh's figures suggest that, contrary to what the original description states, the black spots on the dorsal surface do not seem to form "longitudinal lines." The preserved types currently are colorless, although some faded dark patches can be observed on the ventral surface and the dorsal surface. The small granulations mentioned in the original description are not caryophyllidia. They are simple, conical or rounded tubercles, with spicules protruding without any regular arrangement. Also, the original description indicated that animals would autotomize part of their mantle when put in alcohol. This might explain the current condition of the specimens #1 and #2 (body walls with no lateral dorsal notum). The original description did not include a clear description of the oral tentacles: all types examined have digitiform, ungrooved oral tentacles. The anterior foot is described as bilabiate: indeed, the anterior foot is bilabiate with the upper lip notched.

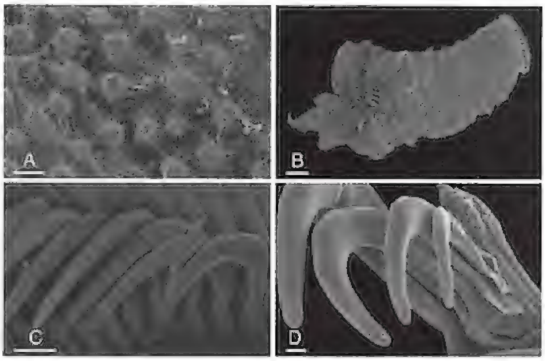

FIGURE 274. *Discodorididae crucis*, lectotype (type specimen #1) and/or paralectotype (type specimen #2), ZMUC. A. Dorsal notum, tubercles, scale = 200 µm.— B. Part of the radula, scale = 400 µm.— C. Median teeth, scale = 100 µm.— D. Outermost teeth, scale = 20 µm. Note that the radula and the notum may be part of the lectotype (type specimen #1), a paralectotype (type specimen #2), or both.

The piece of radula prepared for SEM probably includes only part of the right half of the radula (15 half rows and about 25/30 teeth per half row). The innermost teeth may be absent. Teeth are hamate, including the outermost ones, with no denticles. This piece of radula could be part of the material studied by Bergh (1879b, 1880a), who mentioned a radular formula of 22/25 × (49/50-0-49/50).

DISCUSSION.— Although not brief, Bergh's (1879b, 1880a) re-description of two types collected by Riise from St. Thomas (most likely the type specimens #1 and #2) is largely uninformative. Bergh mentioned several general characters, such as the anterior bilabiate foot with a notched upper lip, two digitiform oral tentacles, rhinophores with forty lamellae, hamate teeth (represented on five figures that he published in 1878 under the name *Discodoris crucis*), but he did not mention any internal characters that could help us re-identify *crucis*. However, the anatomy of one paralectotype (specimens #3) dissected for the present study is hardly compatible with Bergh's re-description of *crucis*. Bergh described an unarmed, 2 mm long penis (in a fully mature reproductive system), whereas the penis of specimen #3, much longer and armed with numerous strong hooks, is diagnostic of *Discodorididae branneri*.

One would think that the hooks of the penis of *branneri* could hardly be overlooked. However, Bergh overlooked them in the penis of two type specimens of *notha*. The type material of *notha*, a *Discodoris* species described by Bergh (1877a) from the Caribbean Sea (Guadeloupe and St. Thomas) includes four specimens, two of which (from Guadeloupe) are part of *Discodorididae* *branneri* (see *Discodorididae notha* and *Discodorididae branneri*). Interestingly, these two specimens collected by Schramm from Guadeloupe had been identified as *D.* (for *Doris*) *crucis* by Mörch, until Bergh decided to include them in a new species, *notha*. My point is that Bergh did not mention the strongly armed penis present in these two specimens. Therefore, there is a chance that Bergh also overlooked the hooks of the penis of the two types of *crucis* that he dissected. However, the penis described by Bergh in *crucis* would be of an exceptionally small size (2 mm) for two fully mature individuals of *branneri*. Therefore, it is more likely that the specimens dissected by Bergh did not have a *branneri*-like penis and were not part of *branneri*.

Unfortunately, it is still unclear what this other entity was. It could be *Tayuva lilacina* (referred to as *hummelincki* in the Caribbean): after all, Marcus and Marcus missed the jaws when they described *hummelincki* —note that Bergh classified *crucis* in *Discodoris* in 1879 because he created *Peltodoris* two years later, in 1880. The fact that the specimen #4, not dissected by Bergh, is part of *lilacina* does not imply necessarily that the two other specimens (specimens #1 and #2) that he dissected are also part of *lilacina*. These specimens #1 and #2 could be part of *lilacina* or another species: neither Mörch's original description, nor Bergh's re-description can help us re-identify the species that specimens #1 and #2 are part of.

In conclusion, *Discodorididae crucis* is regarded as a *nomen dubium* because specimens could hardly be identified as *crucis*. The Caribbean fauna is still poorly known and poorly represented in collections; even if future collections from the Virgin Islands provide new specimens that could fit with Bergh's re-description of *crucis*, it will remain difficult to identify them as *crucis* for sure. Finally, Eliot (1906e:142) argued that that *crucis* could be the same species as *Peltodoris sauvagei* Rochebrune, 1881, from the Cape Verde Islands. The color of *sauvagei* (green dorsal notum and purple gills) is quite different from the color of *crucis*, but the vague description of the *crucis* is potentially compatible with many species.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *crucis* shows that *crucis* does not belong to *Discodoris*. It is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial for *crucis* should be *"Metadiscodoris" crucis*. Possible names under the *ICPN* are *"Metadiscodoris" crucis* or simply *Discodorididae crucis*. This species, like several others, simply lacks the sufficient data to be placed by a phylogenetic test (see Introduction).

"*Montereina*" *erubescens* (Bergh, 1884) New combination
Discodorididae erubescens (Bergh, 1884) New combination

Figure 275.

Discodoris ? erubescens Bergh, 1884b:662-665, plate LXIX, figs 19-28.

TYPE MATERIAL.— The holotype, by monotypy, could not be found. The holotype could not be found and is probably lost.

TYPE LOCALITY.— Zoological Station, Trieste, Adriatic Sea.

DISTRIBUTION.— The holotype is the only specimen known.

LITERATURE.— Several authors (Carus 1893:221; O'Donoghue 1929:764; Nordsieck 1972:62; Costello et al. 2001:202) have mentioned the existence of *Discodoris erubescens* in checklists of Mediterranean species, without adding data or commenting on Bergh's description. Pruvot-Fol (1954a:273) mentioned *erubescens* as one of the four species of *Discodoris* present in the Mediterranean, and briefly pointed out that the color and the notum morphology should help people re-identify it. Marcus and Marcus (1963:31) mentioned the presence of denticles on the hook of the last outermost teeth of *erubescens*. Finally, Marcus and Marcus (1967a:80) briefly pointed out the "color, white with reddish hue alive and 12 bipinnate gills" of *Discodoris erubescens*.

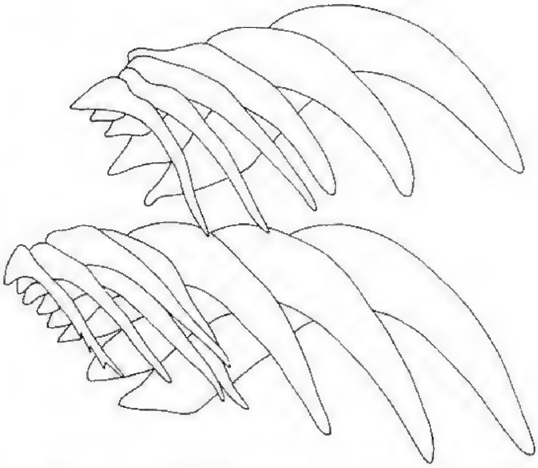

Figure 275. *Discodorididae erubescens*, radular teeth, after Bergh (1884: plate LXIX, fig. 25).

Remarks on the original description (Fig. 275).— According to Graeffe's field notes, the live animal was white with a pinkish-reddish hue. Preserved, the specimens measured 20/11.5 mm. Bergh described some general features, such as the notched upper lip of the bilabiate, anterior foot, the digitiform oral tentacles, 25 rhinophoral lamellae, two jaw plates, and a radular formula of 23 × (23-0-23) with hamate teeth. However, the branchial sheath and plumes are unusual: there are twelve bipinnate branchial plumes; the gill opening is kidney-shaped because of a lid-like structure that almost closes the opening. Bergh's illustration of the dorsal tubercles does not help us determine whether or not those tubercles were caryophyllidia. Finally, in some rows, the hook of the outermost tooth bears from one to three denticles, which Bergh regarded as abnormal structures (because not present in all rows).

Discussion.— One can hope that sooner or later new specimens will be collected from the type locality, or the Mediterranean. It seems that *erubescens* has not been redescribed since Bergh's original description. Several features (gill opening, bipinnate plumes, color) should help people re-identify *erubescens*, which is why it is not regarded here as a *nomen dubium*. The presence of twelve bipinnate branchial plumes is unusual in discodorids (see, e.g., *Discodorididae greeleyi*). Note that another species from the same biogeographic province *Baptodoris perezi* Llera and Ortea *in* Ortea, Perez and Llera, 1981, from the Canary Islands, also has twelve bipinnate gills, but seems to differ from *erubescens* for the color, the shape of the gill opening, and the absence of denticles on the outermost radular teeth. However, these characters vary among individuals (except for the shape of the gill opening that is quite unusual in *erubescens*). Note, also, that Pruvot-Fol's (1951:9-10, plate II, fig. 10) *Atagema gibba* was also originally described with some sort of a lid (divided in three valves though) over the branchial opening, but *Atagema gibba* is not a pinkish animal, and the two names likely refer to two distinct species.

Supra-specific relationships.— Bergh carefully and rightly indicated in the original description that the classification of *erubescens* in *Discodoris* was questionable. Step by step, however, this uncertainty has disappeared in the literature: Carus (1893) mentioned *Discodoris* ? *erubescens*; Pruvot-Fol (1954) mentioned *Discodoris* ? *erubescens* as well, but thought that there was no doubt that *erubescens* was part of *Discodoris*; O'Donoghue (1929), Marcus and Marcus (1963, 1967a), and Costello et al. (2001) just mentioned *Discodoris erubescens*, with no question mark.

A phylogenetic test of the relationships of *erubescens* shows that *erubescens* does not belong to *Discodoris*. It is part of the metaphyletic group at the base of *Discodorididae* (largely because of the lack of sufficient data). The Linnaean binomial for *erubescens* should be *"Montereina" erubescens*. Possible names under the *ICPN* are *"Montereina" erubescens* or simply *Discodorididae erubescens*.

"*Montereina*" *flindersi* (Burn, 1962) New combination
Discodorididae flindersi (Burn, 1962) New combination

Figure 276.

Anisodoris flindersi Burn, 1962:159-160, text figs 10-12, plate 1, figs 6-7.

Type material.— Holotype (NMV F17482), by monotypy: one specimen 24/15 mm preserved (curved body), leg. J. H. Macpherson, 16 February 1956.

Type material condition.— The holotype was dissected by Burn. The body wall remains, with some pieces of the digestive system and reproductive system (largely destroyed; spermatic pouches are missing).

Type locality.— Spencer Gulf, Peak Bay, South Australia.

Distribution.— The holotype is the only specimen known.

Habitat.— Intertidal zone.

Remarks on the original description (Fig. 276).— The specimen described as dark grayish brown currently is dirty grayish. Burn described a pale yellow hyponotum and a yellow foot with orange margins. The ventral surface currently is colorless, dirty cream. Bergh mentioned "low soft pustules" on the dorsal notum. These pustules resemble to *Carminodoris*-like tubercles, large, low (though more elevated on the edges), and not densely arranged upon the notum. Burn mentioned six branchial plumes and at least seven rhinophoral lamellae (their exact number could not be determined). The anterior foot is bilabiate. Contrary to what Burn described, the upper lip is clearly notched. The left oral tentacle is digitiform; the right tentacle is missing. The stomach is narrow, median, instead of large and free on top of the digestive gland. The labial cuticle is smooth. The radular features could not be verified because the slide with the radula is missing: a radulae formula of 25 × (38-0-38), all teeth hamate. Burn's description of the reproductive system is confusing, and nothing could be verified about the genital anatomy because the reproductive system is largely destroyed (were found only two unclear prostatic parts, a female gland mass, and some pieces of what could be the deferent duct). Some genital features described by Burn are doubtful: the "large, flat, cushion-shaped" ampulla; the spermatheca (probably the bursa copulatrix) that "enters the female duct at the part regarded by the author as the vagina." It is difficult to imagine how Burn's representation of the reproductive system of *flindersi* could match the organization usually found in *Discodorididae* (unless this species really has an unusual genital anatomy). Burn may have interpreted an accessory vestibular gland as the bursa copulatrix, the bursa copulatrix as the ampulla, etc.

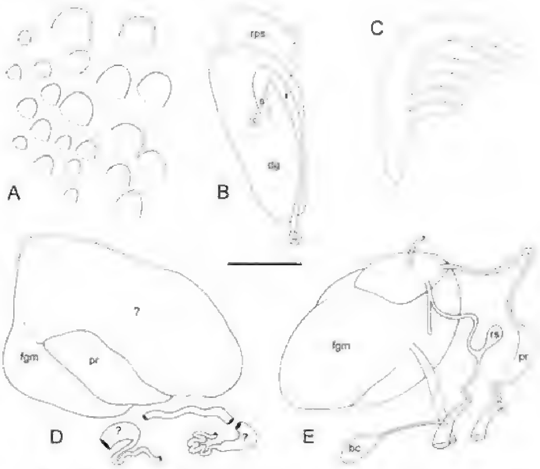

Figure 276. *Discodorididae flindersi*, holotype (MV F17482). A. Dorsal tubercles, scale = 2 mm.— B. Digestive system (except buccal mass), scale = 6 mm.— C. Radular teeth, after Burn (1962: fig. 12).— D. Reproductive system, as currently preserved, scale = 2.4 mm.— E. Reproductive system, after Burn (1962: fig. 11).

Discussion.— The original description of *flindersi* provides so little and so confusing anatomical information that it currently is difficult to determine what this species is. The only character that may help people find new specimens of *flindersi* from South Australia is the presence of large, low tubercles on the dorsal notum. Burn's anatomical description probably will be of little help.

This species is regarded as poorly known, not as a *nomen dubium* because there is some hope for potential re-identification.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *flindersi* shows that *flindersi* does not belong to *Discodoris*. It is part of the metaphyletic group at the base of *Discodorididae* (largely because of the lack of sufficient data). The Linnaean binomial for *erubescens* should be *"Montereina" flindersi*. Possible names under the *ICPN* are *"Montereina" flindersi* or simply *Discodorididae flindersi*.

"*Montereina*" *golaia* (Marcus and Marcus, 1966) New combination
***Discodorididae golaia* (Marcus and Marcus, 1966) New combination**

Figures 277-278.

Discodoris golaia Marcus and Marcus, 1966:179-181, figs 40-42.

TYPE MATERIAL.— Holotype, by monotypy (NMNH 576264, slides F805, F806, F807): one specimen 38/26 mm preserved, [leg. Frederick M. Bayer, aboard R/V Pillsbury], [15 May 1965].

TYPE LOCALITY.— Fernando Póo, 03°45'N, 08°48'E, Gulf of Guinea, eastern Atlantic.

TYPE MATERIAL CONDITION.— Ernst and Eveline Marcus dissected the holotype. The body wall (dorsal notum separated from the body cavity), the gills, and the digestive gland remain in the jar. The reproductive system, the labial cuticle, the radula, and pieces of the notum are preserved on three slides. A piece of notum was prepared for SEM in the present study.

DISTRIBUTION.— So far, *golaia* is only known from the type locality.

REMARKS ON THE ORIGINAL DESCRIPTION (Figs. 277-278).— Unlike Eveline and Ernst Marcus' description in which the dorsal color is brownish, the color is rather cream with many brown spots. A more or less continuous brown ring is adjacent to the foot on the hyponotum. There are 25 to 30 rhinophoral lamellae, and six branchial plumes. The anterior foot is bilabiate and the upper lip is notched. The oral tentacles are digitiform and not grooved. The dorsal tubercles are as described in the original description: broader than high, and flattened above (which might be due to preservation). Eveline and Ernst Marcus mentioned four jaws: there actually are only two lateral jaws, as usual. The radular formula found is 23 × (47-0-47), which is exactly what Eveline and Ernst Marcus described: 23/24 × (47/50-0-47/50). The rachidian space is narrow; the size of teeth gradually increases (ten to fifteen innermost teeth), then remains more or less stable (median teeth), and finally decreases (three or four outermost teeth). All teeth are hamate, and do not seem to bear any denticles. The intestine was cut and the presence of an intestinal loop on the ventral surface of the digestive gland could not be verified. It could not be determined what Marcus meant by "ectal part of the prostate" because the distal part of the prostate is missing on the slide: it could correspond to the second part of the prostate or to some folds in the proximal part of the deferent duct. However, note that Eveline and Ernst

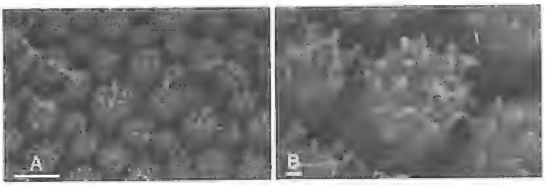

FIGURE 277. *Discodorididae golaia*, holotype, NMNH 576264, dorsal notum, tubercles. A. Scale = 200 µm.— B. Scale = 200 µm.

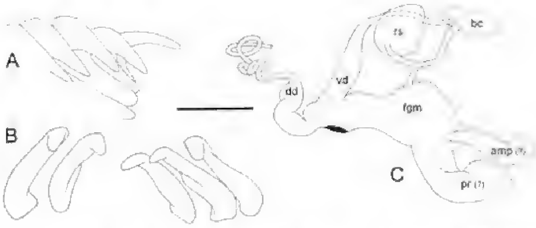

FIGURE 278. *Discodorididae golaia*, holotype, NMNH 576264. A. Outermost radular teeth, as currently preserved, scale = 85 µm.— B. Innermost radular teeth, as currently preserved, scale = 70 µm.— C. Reproductive system, as currently preserved, scale = 2.6 mm.

Marcus (e.g., 1967a:79) sometimes designated the second prostatic part as the 'ectal part' of the prostate; but they may have used this expression here to designate a proximal folded deferent duct, as in *Sebadoris fragilis*. The deferent duct is tightly convoluted, and the fertilization and vaginal ducts are straight. The original description is vague about the presence of a penial papilla: No penial organ was seen on the slide.

Discussion.— The original description of *golaia* is general and does not provide any diagnostic feature that could help us re-identify this species. The color pattern of *golaia* is by no means diagnostic. However, only the preserved color of *golaia* is currently known and the color of live animals might be more useful for identification purposes. The presence of simply hamate teeth and the radular formula of 23-(47-0-47) are not helpful either. Also, the tri-dimensional organization of the reproductive system and the shape of the penial papilla (if there is any) are unknown. Finally, the tubercles might be flattened due to preservation. One can reasonably hope that new specimens from the type locality will be collected. However, it will be hard to determine whether or not new specimens are part of the same species as the holotype of *golaia* because of the absence of clearly distinctive feature in that holotype. In conclusion, *golaia* is regarded as a poorly known species, but it could less conservatively be regarded as a *nomen dubium* as well.

Supra-specific relationships.— A phylogenetic test of the relationships of *golaia* shows that *golaia* does not belong to *Discodoris*. It is part of the metaphyletic group at the base of *Discodorididae* (largely because of the lack of sufficient data). The Linnaean binomial for *golaia* should be *"Montereina" golaia*. Possible names under the *ICPN* are *"Montereina" golaia* or simply *Discodorididae golaia*.

"Montereina" greeleyi (MacFarland, 1909) New combination
Discodorididae greeleyi (MacFarland, 1909) New combination

Figures 279-280.

Peltodoris greeleyi MacFarland, 1909:84-88, plate XV, figs 77-82.— Marcus, 1955:137-140, plate 14, figs 126-132.— Marcus and Marcus, 1967a:66, 72-74, 124, figs 94-98.— Eyster, 1980:588, fig. 3A-B.
Diaulula greeleyi.— Camacho-García and Valdés, 2003:71-75, figs 1C, 4-5.
Peltodoris nayarita Ortea and Llera, 1981:47-52, figs 1-4.— Bertsch et al. 2000:100.— Camacho-García et al. 2005:85, unnumbered figure.

Type material (*greeleyi*).— Holotype, by monotypy (CASIZ 021021, 21 slides): one specimen 18/10 mm preserved, leg. A. W. Greeley [Branner-Agassiz Expedition], 28 July 1899.

Type material (*nayarita*).— Holotype, by original designation (MNHN, no catalogue number): one specimen 14/7 mm preserved, [leg. unknown], 1980. Not examined for the present study.

Type locality (*greeleyi*).— Riacho Doce, Alagoas, Brazil.

Type locality (*nayarita*).— Isabel Island, 21°52′N, 105°54′W, Nayarit, Mexico.

Type material condition (*greeleyi*).— Frank M. MacFarland entirely dissected the holotype. Only some pieces of the body wall, the thirteen unipinnate branchial plumes, the stomach, and some pieces of the digestive gland remain. However, the slides that accompany the specimen include most of the internal organs: twelve slides with mantle preparations, one with mantle spicules, one with the nervous system, one with the buccal ganglia, one with a rhinophore, one with the radula, one with a salivary gland, one with an unidentified membrane, one with the albumen gland, one with the penis and the vagina. A piece of notum was prepared for SEM in the present study. Note that the type material is incomplete (especially the reproductive system) because it was "being dissected at the time of the earthquake of April 18, 1906 [this major earthquake destroyed most of San Francisco, including the building of the California Academy of Sciences]."

Type material condition (*nayarita*).— Unknown.

Additional material dissected.— **Brazil**, Ubatuba, [collecting date unknown, before January 1976], five specimens 7/4 (#1) [dissected], 6/4 (#2) [SEM picture of the whole animal], 5/2 (#3) [dissected], 4/2 (#4) [not dissected], and 3/2 (#5) [not dissected], mm preserved, leg. Eveline Marcus, identified as *Peltodoris greeleyi* by Ev. Marcus or M. P. Morse (MCZ 288303) [these specimens were poorly preserved and the reproductive system could not be examined; also, note that these specimens are not vouchers of specimens described by Marcus in 1955 because Ubatuba is not the same locality as São Sebastião Island, although it is close to it].

Distribution.— So far, *greeleyi* is known from the Western Atlantic: Brazil (MacFarland 1909; Marcus 1955; present study), Florida (Marcus and Marcus 1967a), and South Carolina (Eyster 1980). It also is known from the Eastern Pacific: Nayarit, Mexico (type locality of *nayarita*), Punta Eugenia, Baja California (Bertsch et al. 2000), and Costa Rica (Camacho-García and Valdés 2003).

Literature.— The anatomy of the holotype of *greeleyi* was thoroughly described by MacFarland (1909). The description of the holotype of *nayarita* by Ortea and Llera (1981) lacks SEM pictures and precise drawings. Marcus (1955) and Marcus and Marcus (1967a) have published additional anatomical data. However, the infra-specific variation is still unknown, at least for the internal anatomy: Camacho-García and Valdés (2003) examined multiple specimens but provided anatomical data just for a single specimen (INB0001496508). Camacho-García et al. (2005) published a color picture of the dorsal notum.

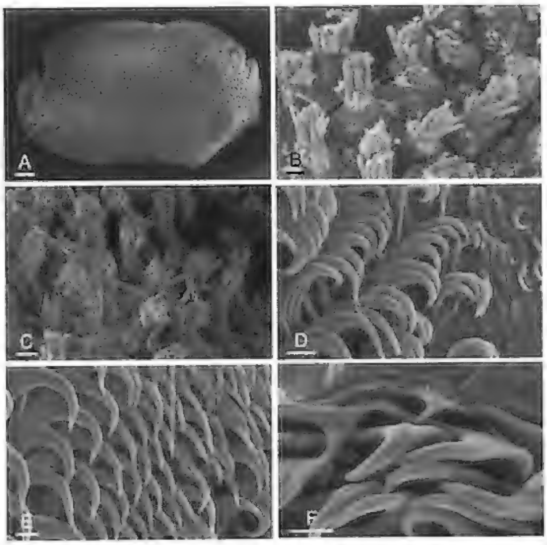

Figure 279. *Discodorididae greeleyi*. A. Dorsal view, MCZ 288303 (#2), scale = 400 µm.— B. Dorsal notum, caryophyllidia, MCZ 288303 (#2), scale = 200 µm.— C. Dorsal notum, holotype, CASIZ 021021, scale = 200 µm.— D. Innermost teeth, MCZ 288303 (#1), scale = 10 µm.— E. Median teeth, MCZ 288303 (#1), scale = 10 µm.— F. Outermost teeth, MCZ 288303 (#1), scale = 10 µm.

Remarks on the original description (*greeleyi*, Figs. 279C, 280A-C).— The original description of *greeleyi* is complete, as usual with MacFarland. However, it is based on a single specimen, and individual variation was not addressed. The color of the preserved animal was pinkish; the pieces of the mantle are now whitish. The notum is "villous, quite velvety to the touch and quite similar to *Diaulula* in this respect." Caryophyllidia are clearly present, though poorly preserved. There are 16 rhinophoral lamellae, and 13, "simply pinnate" branchial plumes. The anterior foot is bilabiate and the upper lip is notched. The oral tentacles were not described by MacFarland. The labial cuticle is smooth. MacFarland gives a radular formula of 49 × (60-0-60), for a 18 mm long specimen (preserved). It seems that there are fewer teeth per row and fewer rows, i.e., *c.* 30 × (45-0-45), but both teeth and rows are difficult to count. Important detail, the rachidian space is narrow; the size of teeth gradually increases (ten innermost teeth), then remains more or less stable (median teeth), and finally decreases (five outermost teeth). All teeth are hamate, and do not bear any denticles. Some features of the reproductive system may be emphasized: the bursa copulatrix is much bigger (about ten times) than the receptaculum seminis; the vas deferens presents an "irregular loop;" a "cylindrico-conical glans penis" is protected by a praeputium. According to MacFarland, its length is 0.78 mm, but it seems to be shorter. Given its size and shape, it is not impossible that it simply corresponds to the distal portion of the vas deferens, although it might be an independent penis (because several discodorids have small, conical, copulatory organs).

Remarks on the original description (*nayarita*, Fig. 280D).— The original description is exclusively based on a single specimen, and individual variation was not addressed. The animal was yellow, with small darker spots on the dorsal notum, especially in the center. Caryophyllidia are present. The rhinophores are dark brown. The anterior foot is bilabiate and the upper lip is notched. There are eight unipinnate branchial plumes (instead of 13 in *greeleyi*). The labial cuticle is smooth. Ortea and Llera give a radular formula of 51 × (50-0-50). Ortea and Llera's description of the reproductive system is brief and the drawing schematic, however, a few features can be pointed out here: the bursa copulatrix is not much bigger (about four times) than the receptaculum seminis; the vas deferens is loosely convolued; there seems to be no distinct penis.

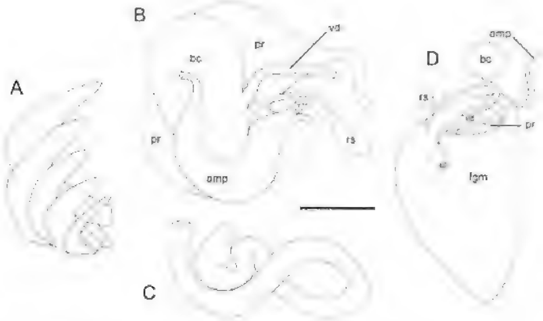

FIGURE 280. *Discodorididae greeleyi*. A. Outermost radular teeth, holotype, as currently preserved, scale = 60 µm.— B. Reproductive system, holotype, after MacFarland (1909: plate XV, fig. 82).— C. Penial papilla, holotype, as currently preserved, scale = 400 µm.— D. Reproductive system, *Peltodoris nayarita*, holotype, after Ortea and Llera (1981: fig. 4), scale = 1 mm.

Description of new specimens (Fig. 279A-B, D-F).— The color of the animals dissected here is unknown, but the preserved animals are homogeneously grayish. The dorsal notum bears caryophyllidia. There are about ten rhinophoral lamellae. There are 9 or 10 branchial plumes, clearly unipinnate. The anterior foot is bilabiate and the upper lip is notched. The oral tentacles are digitiform and not grooved. In the digestive system, the intestine is dorsal and straight. The radular formula is 25 × (25-0-25) in a 7 mm long preserved specimen. Nothing could be observed in the reproductive system due to the poor preservation of the specimens and the fact that they were probably immature.

Diagnostic features.— The most diagnostic feature of *greeleyi* clearly is the presence of unipinnate branchial plumes, although their number varies (see below), as well as the dorsal color (see, Camacho-García et al., 2005).

Infra-specific character variation.— Few data are available about the infra-specific character variation since no one has yet described multiple specimens of various ages, from different populations and regions. However, a few features can be discussed. The largest specimen, alive, was found in Florida (Marcus and Marcus 1967a): it measured 35 mm in length and 29 mm in width. Note that the maximum size of the 82 specimens listed by Camacho-García and Valdés (2003) from the Pacific coast of Costa Rica is 16 mm and that many specimens measure less than 10 mm. The color does seem to vary: yellow (original description of *nayarita*), pale yellow to orange (Camacho-García and Valdés 2003), orange red (Bertsch et al. 2000), light brown (Marcus and Marcus 1967a), and brown (Eyster 1980). It seems that the number of branchial plumes varies: from 8 plumes (in the holotype of *nayarita*) up to 14 plumes (Marcus and Marcus 1967a). It is unclear whether the presence of 12 plumes mentioned by Camacho-García and Valdés (2003) refers to the 82 specimens that they examined or just to the specimen that they described anatomically (INB0001496508). The radular formula varies as well, as expected: from 25 × (25-0-25) in a 7 mm long preserved specimen (present study) up to 25 × (25-0-25) in a 35 mm long, living specimen (Marcus and Marcus 1967a). Marcus and Marcus (1967a) mentioned a false rachidian plate, also found occasionally (e.g., *lilacina*, CASIZ 121234). In the reproductive system, the deferent duct is consistently loosely convoluted; the relative size of the two spermatic pouches varies, the bursa copulatrix being much larger (MacFarland 1909; Camacho-García and Valdés 2003) or just twice as big as the receptaculum seminis (Marcus and Marcus 1967a); the presence (MacFarland 1909; Marcus and Marcus 1967a) or absence (Camacho-García and Valdés 2003) of a distinct conical penis could be explained by the fact that this copulatory organ is just an evaginable portion of the deferent duct (in which case it could be absent or present), or by the fact that some authors overlooked it.

Discussion.— The main question about *greeleyi* is of course whether there is just one species present in eastern Pacific and western Atlantic, or two species. It seems that we do not have enough data to answer this question at present. Anatomically, it is clear that the few specimens described so far (i.e., one specimen from Costa Rica by Camacho-García and Valdés; one specimen from Brazil by MacFarland; four specimens from Brazil by Marcus; one specimen from Florida by Marcus and Marcus; plus two specimens incompletely described by Eyster from South Carolina and here from Brazil) are similar. However, unless somebody actually describes the anatomy of multiple specimens from different regions, it might be difficult to decide whether or not there are diagnostic features that separate the populations from the eastern Pacific and the western Atlantic. In other words, our current inability to distinguish specimens from eastern Pacific and the western Atlantic should certainly not be regarded as a final word. Also, it is worth pointing out that even in the absence of any morphological or anatomical clear difference between specimens from eastern Pacific and the western Atlantic, there could still be two sibling species, impossible to distinguish but reproductively isolated nonetheless. The synonymy between *greeleyi* and *nayarita* proposed by Camacho-García and Valdés needs to be addressed with non-morphological tools.

Supra-specific relationships.— Two supra-specific affinities have been proposed so far for *greeleyi* (*Peltodoris* and *Diaulula*), none of them supported by phylogenetic analyses. A phylogenetic test of the relationships of *greeleyi* shows that it does not belong to the clade *Peltodoris*, but instead is part of a metaphyletic group at the base of *Discodorididae*. Also, no synapomorphies could be found for *Diaulula* (and nobody else has ever demonstrated that *Diaulula* was a clade): the generic name *Diaulula* has been used for caryophyllidia-bearing dorids that do not positively belong to any other genera of caryophyllidia-bearing dorids. The Linnaean binomial for *greeleyi* should be "*Montereina*" *greeleyi*: *Discodoris greeleyi* and *Diaulula greeleyi* are both phylogenetically inaccurate because *greeleyi* does not belong to *Discodoris* and because *Diaulula* is not a clade. Possible names under *ICPN* are "*Montereina*" *greeleyi* or simply *Discodorididae greeleyi*.

"*Montereina*" *igla* (Marcus and Marcus, 1967) New combination
Discodorididae igla (Marcus and Marcus, 1967) New combination

Figure 281.

Peltodoris hummelincki igla Marcus and Marcus, 1967b:598, 617-621, figs 45-47.— Marcus, 1976a:139-140, 142, fig. 28.

Type material.— Holotype (NMNH 836764), by monotypy: one specimen 35/15 mm preserved, leg. Frederick M. Bayer, 9 July 1966.

Type locality.— 09°37.30′N, 78°54′W, 67-123 meters depth [station 330, R/V Pillsbury expedition, off the Atlantic coasts of Colombia and Panama, organized by the Dr. Frederick M. Bayer and other staff members of the Institute of Marine Science], off Colombia, Caribbean Sea.

Type material condition.— The type was entirely dissected by Eveline and Ernst Marcus. Only the body wall and the digestive gland remain in the jar. No slides could be found.

Distribution.— Caribbean Sea, off the Atlantic coasts of Colombia (type locality) and Santa Marta Island (Marcus 1976a).

Occurence.— So far, *igla* is only known from the holotype and three additional specimens from Santa Marta Island.

Remarks on the original description (Fig. 281).— The color of the preserved animal was described as: "light brownish grey with darker flecks, about 1 mm in diameter. These flecks are formed by subepidermal pigment cells. Some small spots around the area of the visceral hump are especially dark." The sole is white. The preserved animal measured 30/16.5 mm. The tubercles (called "short papillae" by the Marcus) are not caryophyllidia. Tubercles were described in detail: "They are full of spicules, so that the aspect differs considerably from the typical form. Some chromatophores in the papillae and under them produce the general color. The spicules stand out over the tip of the papillae." SEM pictures of a piece of notum were taken for the present study: although the notum was largely destroyed, these pictures confirmed that the tubercles are not caryophillidia. Some general features shared by all discodoridids were described, such as two digitiform oral tentacles and a bilabiate anterior foot with a notched superior lip. Some general morphological and anatomical features for this species were described as well, such as 25 rhinophoral lamellae, six brown tripinnate branchial plumes, and a smooth labial cuticle. The radular formula included 39 teeth per half-row, but the number of rows was not specified. The lateral teeth were described as "evenly rounded, so that base and cusp are indistinguishable." The stomach is free. The reproductive system was probably immature, especially the female glands. According to their drawing, there is no muscular wall protecting the distal area of the reproductive system, although the Marcus described a "heavily muscular male atrium" that could possibly (but hypothetically) be interpreted as a muscular wall. The deferent duct is narrow and unfolded. Both the deferent duct and the vaginal duct are long and convoluted. A simple penial papilla was described, but no distinct penis.

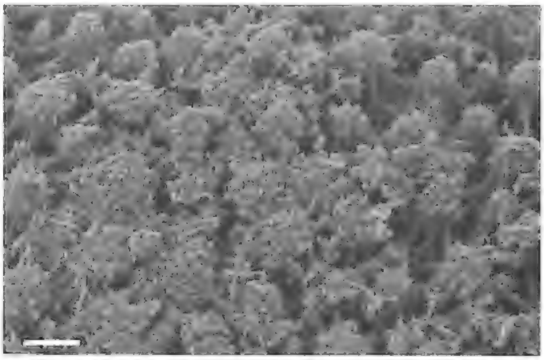
Figure 281. *Discodorididae igla*, dorsal notum, holotype, NMNH 836764, scale = 100 µm.

Discussion.— The original description of *hummelincki igla* was not brief. However, it did not provide any character that could help us understand why *hummelincki igla* was part of *hummelincki* (here a synonym of *Tayuva lilacina*). Indeed, the type specimen of *hummelincki igla* lacks the most critical features that are diagnostic of *hummelincki*, in particular the penis. Moreover, it presents anatomical details that are beyond the limits of the variation expected for this species, such as highly convoluted vaginal duct and deferent duct. A few years later, Eveline Marcus identified three specimens (two of which were 50 mm long, preserved) from the Santa Marta Island, off Colombia, as *hummelincki igla*. They had peculiar salivary glands. However, the fact that they are part of *hummelincki igla*, or even *hummelincki*, i.e., *lilacina*, is uncertain. Generally speaking, the Marcus had little chance to rediscover specimens of *hummelincki*, because they thought that the labial cuticle of *Peltodoris hummelincki* (i.e., *Tayuva lilacina*) was smooth, and therefore the new specimens of "*hummelincki*" would necessarily have a smooth labial cuticle too. However, we know now that the labial cuticle of *lilacina* is armed with jaw plates. As a consequence, the real specimens of "*hummelincki*" were identified by the Marcus as *Tayuva ketos gila*, whereas the specimens they called *Peltodoris hummelincki igla* would not be part of *hummelincki*, which, again, is a synonym of *Tayuva lilacina*… Although *Discodorididae hummelincki igla* likely is not part of

Tayuva lilacina, it is difficult to say what it is: even if new specimens are collected from the type locality, *igla* will hardly be identifiable. Therefore, *igla* is regarded here as a *nomen dubium*.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *igla* shows that it does not belong to the clade *Peltodoris*. It is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial name for *igla* should thus be *"Montereina" igla*. Possible names under the *ICPN* are *"Montereina" igla* or simply *Discodorididae igla*.

"*Montereina*" *labifera* (Abraham, 1877) New combination
***Discodorididae labifera* (Abraham, 1877) New combination**

Figures 282-286.

Doris labifera Abraham, 1877:205, 254, plate XXIX, figs 13-14.
Discodoris labifera.— Farran, 1905:330, 335-336, plate I, figs 17-18.

TYPE MATERIAL.— Three syntypes (NHM 1869.6.12.8a, b, c): one specimen 26/12 mm preserved, leg. E. P. Wright, [no collecting date], [this specimen was labeled as the holotype - NHM 1869.6.12.8a]; two specimens 26/15 and 30/17 mm preserved, leg. E. P. Wright, [no collecting date], [these two specimens were labeled as paratypes - NHM 1869.6.12.8b, c]. These three type specimens are syntypes because Abraham did not designate a holotype. There is no particular reason to designate a lectotype.

TYPE LOCALITY.— Seychelles, Indian Ocean.

TYPE MATERIAL CONDITION.— One syntype (NHM 1869.6.12.8a), which was probably dried for a while and then transferred to alcohol, is in a poor condition. One of the two other syntypes (NHM 1869.6.12.8b, c), however, was still entire and well preserved externally (the 26 mm long specimen). It was dissected for the present study (the morphological description below is entirely based on this 26 mm long specimen): the internal organs were poorly fixed and the dissection was difficult. The other one (the 30 mm long specimen) had not been dissected either: its oral tube was cut prior to the present study, and the labial cuticle and the radula may have been taken out.

DISTRIBUTION.— Seychelles (type locality), and hypothetically Ceylon.

OCCURENCE.— So far, only three syntypes are known. The three additional specimens mentioned by Farran (1905) from Ceylon are suspicious (see discussion).

LITERATURE.— Abraham's (1877) description only provides some vague information about the color and the external morphology, and a number of 19 rows for the radula. Farran (1905) published two drawings of the radula of a specimen that he identified as *labifera*, but these drawings are poorly informative. Note that Bergh (1878a) mentioned the name *Doris labifera* and indicated with a question mark that he did not know where to classify it.

REMARKS ON THE ORIGINAL DESCRIPTION (Fig. 282).— Abraham's description is brief and largely incomplete. The dorsal color was described as creamish-yellowish with darker spots lightened with preservation. The color of living specimens was unknown (and still is). The hyponotum, the lateral side of the foot and the foot sole bear numerous dark dots.

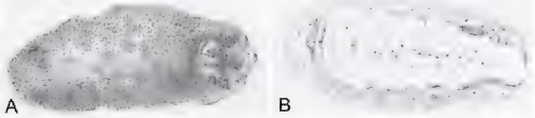

FIGURE 282. *Discodorididae labifera*, original illustrations. A. Dorsal view (Abraham 1877: plate XXIX, fig. 13).— B. Ventral view, from original description of *Doris labifera* (Abraham 1877: plate XXIX, fig. 13).

DESCRIPTION OF A SYNTYPE (Figs. 283-286).— *Color*: The color of the living animal is unknown. The ground color of the dorsal notum is currently tan-whitish, bearing irregularly round darker spots. The ventral surface (hyponotum and foot) is creamish as well.

External morphology. The body is oval. The length equals less than twice the width. The foot

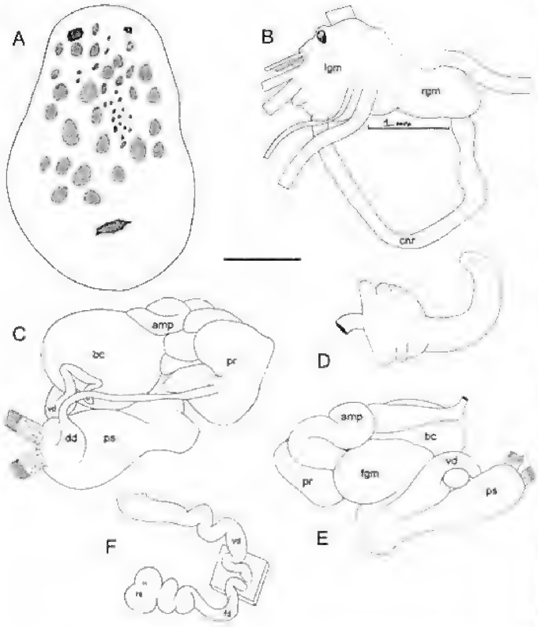

FIGURE 284. *Discodorididae labifera*, syntype. A. Dorsal view, as currently preserved, total length = 26 mm.— B. Nervous system, scale = 1 mm.— C. Reproductive system, scale = 1.2 mm.— D. Penis, total length = 1.7 mm.— E. Reproductive system, scale = 1.3 mm.— F. Spermatic ducts, scale = 1.2 mm.

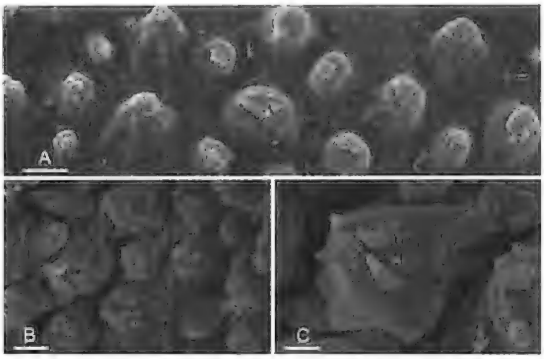

FIGURE 283. *Discodorididae labifera*, dorsal notum, syntype, NHM 1869.6.12.8. A. Scale = 100 µm.— B. Scale = 100 µm.— C. Scale = 30 µm.

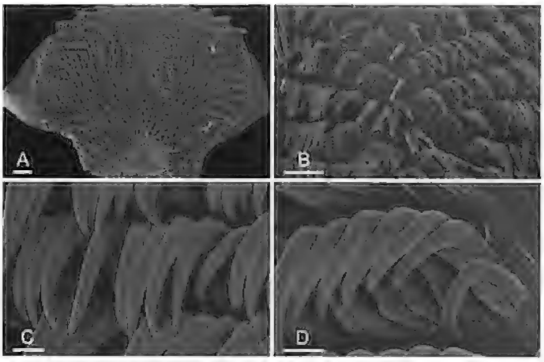

FIGURE 285. *Discodorididae labifera*, radula, syntype, NHM 1869.6.12.8. A. Scale = 200 µm.— B. Innermost teeth, scale = 100 µm.— C. Median teeth, scale = 40 µm.— D. Outermost teeth, scale = 40 µm.

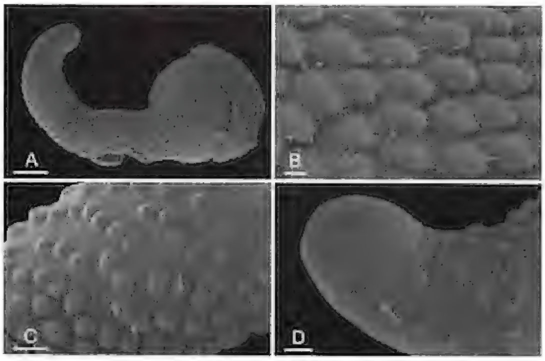

FIGURE 286. *Discodorididae labifera*, penis, syntype, NHM 1869.6.12.8. A. Scale = 200 µm.— B. Scale = 10 µm.— C. Scale = 40 µm.— D. Scale = 40 µm.

is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are flattened and not grooved. The dorsal notum bears non-caryophyllidia tubercles. The edge of the gill opening is smooth, as well as the margin of the rhinophoral sheaths. Small holes (diameter < 10 µm) and small tufts of cilia could not be observed on the mantle, probably due to preservation. There are six tripinnate branchial plumes arranged in circle around the anus. The rhinophores have about 25 lamellae.

Digestive system. The stomach is large, free, on top of the left anterior side of the digestive gland. A small caecum is located on the left posterior side of the stomach. The intestine is straight and dorsal. The labial cuticle is armed with one pair of symmetrical jaws. The radular sac cannot be seen by dorsal dissection. The length of the radula equals less than twice its width. The radular formula is 23 × (45-0-45) in a 26 mm long specimen. The rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the six or eight innermost teeth whose size increases gradually and the last three of four outermost ones whose size decreases gradually. All teeth are hamate, including the outermost teeth. The teeth are not grooved, nor are they denticulate.

Nervous system. Because of poor preservation, the nervous system could not be extracted entirely. The length of the circumesophagal nerve ring equals approximately two or three times the width of the cerebro-pleural ganglia.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is convoluted, with two tight and short loops before reaching the female gland mass. The division between male and female ducts (hidden within the female gland mass) could not be seen by dissection. The flattened prostate is divided in two parts, a proximal whitish part and a distal yellowish part. The straight deferent duct ends in a penis protected by a penial sheath. The penis, 1.7 mm in length, curved and sausage-like, with a broader base though, is entirely covered with small papillae (except at the apex). The vaginal duct is convoluted, with four loose loops. Its distal part is wide. The deferent duct and the vaginal duct join together and form a vestibule not clearly separated from the female duct. The fertilization duct is loosely convoluted (it presents two short loops). The connection between the fertilization duct and the female gland mass, marked by no distinct duct, could not be observed. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is hidden by the receptaculum seminis and the vaginal duct. The bursa copulatrix is about five times larger than the receptaculum seminis. The bursa copulatrix and the receptaculum seminis, both ovate, are attached to one another, although, externally, they seem to be separated by the vaginal duct. Also, the proximal end of the duct of the receptaculum seminis is large and is hardly distinguishable from the receptaculum seminis itself.

DIAGNOSTIC FEATURES.— The diagnostic character of *labifera* is the penis, entirely covered with papillae. The color of living specimens is currently unknown. Preserved specimens may easily be confused with other Indo-Pacific species, especially *lilacina* Gould, 1852. These two species may be more easily distinguishable when we know more about the color of living animals.

INFRA-SPECIFIC CHARACTER VARIATION.— Variation among individuals is unknown because the anatomy of *labifera* is known from a single specimen.

DISCUSSION.— At first, the type specimens of *labifera* were interpreted as *Tayuva lilacina*. Externally, these syntypes are similar to preserved specimens of species like *Tayuva lilacina*, *Discodorididae branneri*, etc. (their dorsal notum is creamish for the ground color with darker irregular spots and dots). The dissection of a syntype really was a surprise. The morphology of the penis was totally different from what was expected. No additional material was found for *labifera*, although several specimens with a notum that could match that of *labifera* have been collected in western Indian Ocean (see *Tayuva lilacina*). One would need to go back to the Seychelles and collect more specimens with this dorsal color (light brownish with irregular darker spots). It is not excluded that this penis could represent an aberrant morphology of the widely-distributed *lilacina*. However, the hypothesis according to which *labifera* is a rare species (at least so far) is favored here because the rest of the reproductive system is very different from *lilacina* too (the muscular wall around the atrium and the folded proximal part of the deferent duct present in *lilacina* were not found here). Finally, Farran (1905) described three specimens from Ceylon that he identified as *labifera*. However, we have no guarantee at all that he really looked at specimens belonging to *labifera*. Farran's examination of the type specimens of *labifera* was pointless because it is impossible to find a diagnostic character on the external morphology of the types. Also, the radula of *labifera* is of a general type found in many other discodorid species, and Farran's observation of the radula was not particularly helpful in identifying *labifera*.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *labifera* shows that it does not belong to the clade *Discodoris*. It is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial name for *labifera* should thus be "*Montereina*" *labifera*. Possible names under the *ICPN* are "*Montereina*" *labifera* or simply *Discodorididae labifera*.

"*Montereina*" *lancei* (Millen and Bertsch, 2000) New combination
Discodorididae lancei (Millen and Bertsch, 2000)

Figures 287-288.

Peltodoris lancei Millen and Bertsch, 2000:361-365, figs 1C, 6-7.
Discodorididae lancei.— Dayrat and Gosliner, 2005:205.

TYPE MATERIAL.— Holotype (CASIZ 110807), by original designation: one specimen 55/45 mm preserved, leg. Mike D. Miller, 28 June 1996. Two paratypes: one specimen 60/50 mm preserved, leg Mike D. Miller, 28 June 1996 (CASIZ 118572); one specimen 20/14 mm preserved, leg. Mike D. Miller, 30 June 1997 (CASIZ 118573).

TYPE LOCALITY.— Holotype: Bahía de Los Angeles, 28°57′N, 113°31′W, 7 meters depth, Gulf of California, Baja California, Mexico. Paratype (CASIZ 118572): Bahía de Los Angeles, 29°02.56′N, 113°32.29′W, 7 meters depth, Gulf of California, Baja California, Mexico. Paratype (CASIZ 118573): Punta Gringa, 5 meters depth, Bahia de Los Angeles, Gulf of California, Baja California, Mexico.

TYPE MATERIAL CONDITION.— The holotype and one paratype (CASIZ 118573) are still complete and have never been dissected. One paratype (CASIZ 118572) was dissected by Millen and Bertsch. Pieces of the notum of the paratype CASIZ 118572 and of the holotype were mounted for SEM.

DISTRIBUTION.— So far, this species is only known from the three type specimens.

HABITAT.— Under stones (all specimens).

REMARKS ON THE ORIGINAL DESCRIPTION (Figs. 287-288).— A color picture of a live animal, several SEM pictures, and an informative drawing of the reproductive system are provided. A few features are emphasized here. The color of live animal was orange-brown to reddish orange. All specimens are currently whitish, although the holotype is a little darker, more creamish. The preserved body tends to be ovate, although live animals seem to be more rounded (Millen and Bertsch 2000: fig. 6A). The oral tentacles are digitiform, non-grooved. The anterior foot is bilabiate, with the superior lip notched. Rhinophores consist of about 15 to 20 lamellae. There are six pluripinnate branchial plumes. Caryophyllidia, not described by Millen and Bertsch, are present, although the notum is not well preserved. The radular formula of the paratype dissected by Millen and Bertsch is 28 × (33-0-33), for a 60 mm long specimen. More importantly, the rachidian space is narrow (Millen and Bertsch 2000: fig. 6C). The reproductive system does not have any distinctive feature, and more specimens will need to be dissected if we wish to find out how its general organization is diagnostic of *lancei*. It is worth noticing the presence of a small, unarmed penis.

DIAGNOSTIC FEATURES.— The diagnostic character of *lancei* is the color of the dorsal notum, homogeneously orange-brown to reddish-orange, although we will probably find in the future that this varies among individuals.

INFRA-SPECIFIC CHARACTER VARIATION.— Variation among individuals is unknown because the anatomy of *lancei* is known from a single specimen, and the external morphology is known from only three specimens.

DISCUSSION.— Although *lancei* was described from only three specimens, it seems to be distinct from other discodorids. More data are needed to address the infra-specific character variation.

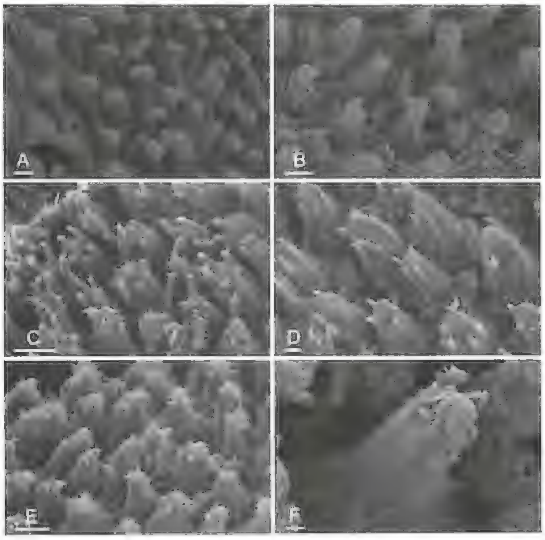

FIGURE 287. *Discodorididae lancei*, notum, types. A. Holotype, CASIZ 110807, scale = 100 µm.— B. Holotype, CASIZ 110807, scale = 100 µm.— C. Paratype, CASIZ 118572, scale = 100 µm.— D. Paratype, CASIZ 118572, scale = 30 µm.— E. Paratype, CASIZ 118572, scale = 100 µm.— F. Paratype, CASIZ 118572, scale = 30 µm.

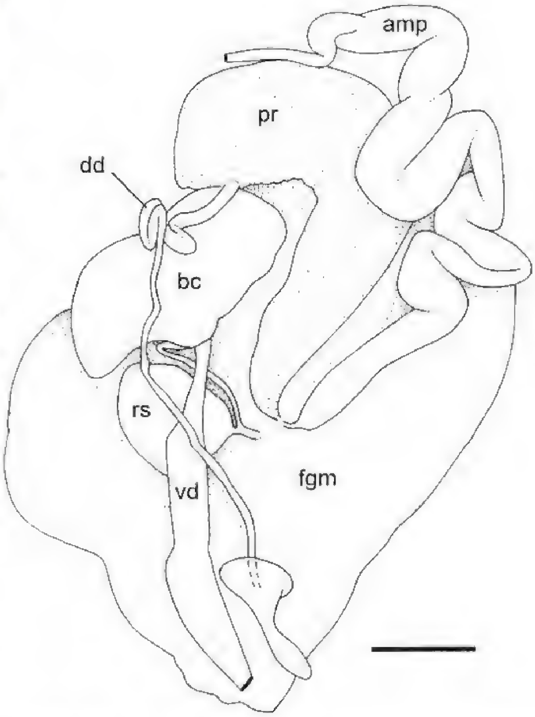

FIGURE 288. *Discodorididae lancei*, reproductive system, after Millen and Bertsch (2000: fig. 7), scale = 3 mm.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *lancei* shows that it does not belong to the clade *Peltodoris*. It is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial name for *lancei* should thus be "*Montereina*" *lancei*. Possible names under the *ICPN* are "*Montereina*" *lancei* or simply *Discodorididae lancei*.

"*Montereina*" *lentiginosa* (Millen, 1982) New combination
***Discodorididae lentiginosa* (Millen, 1982)**

Figures 289-291.

Anisodoris lentiginosa Millen, 1982a:2694-2704, figs 1-6.— Millen, 1982b:17.
Peltodoris lentiginosa.— Behrens, 2004:40.— Behrens and Hermosillo, 2005:74, fig. 142.
Discodorididae lentiginosa.— Dayrat and Gosliner, 2005:205.

TYPE MATERIAL.— Holotype (CASIZ 024099): one specimen 90 mm long (alive) and 75/45 mm preserved, leg. Sandra Millen, 7 July 1977. Five paratypes (two specimens #982.105.1, two specimens #973.7.10, and one specimen #973.246.23) were deposited at the British Columbia Provincial Museum, Victoria, British Columbia, Canada. The paratypes were not examined for the present study.

TYPE LOCALITY.— Dixon Island, Barkley Sound [48°50′N, 125°08′W], 12 meters depth, Vancouver Island, British Columbia, Canada.

TYPE MATERIAL CONDITION.— The holotype, well preserved externally, was not dissected for the present study.

ADDITIONAL MATERIAL DISSECTED.— **Canada**, British Columbia, Barnfield Marine Station, 29 April 2000, two specimens 75/50 [dissected] and 42/25 [not dissected] mm preserved, leg. Mike Blanc, identified as *Anisodoris lentiginosa* by Sandra Millen (CASIZ 168031).

Distribution.— Eastern Pacific, coast of British Columbia, Canada.

Literature.— So far, information about *lentiginosa* was only available from the original description.

Remarks on the original descriptions.— Millen's original description is largely complete. Some features are emphasized briefly commented on. The maximum length of live animals is 180 mm. The color varies from white to pale yellow, with brown blotches irregularly spaced on the dorsal notum, and of various size. The tubercles on the dorsal notum are not caryophyllidia. There are six tetra-pinnate branchial plumes. The digitiform, oral tentacles are not grooved. The upper lip is notched (Millen described it as 'not distinctly notched'). The labial cuticle is smooth. The radular formula is 21/28 × (49/64-0-49/64) in a 57 mm long, preserved specimen. All teeth are smooth. The ampulla is highly convoluted. The prostate is large, flattened, and divided in two parts. The deferent duct is straight. It ends in an "eversible tip 1 mm long, 1 mm wide (…) covered with four or five rows of multifid, platelike spines, 0.3 mm long, 0.45 mm wide." The vaginal duct is wide. The bursa copulatrix is much larger (five times) than the receptaculum seminis. The development is planktotrophic, i.e., the larvae remain in the plankton for 1-1.5 months.

Description of a new specimen (Figs. 289-291).— *Color*. The color of the live animal is unknown. It is currently homogeneously whitish.

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, slightly flattened (probably due to their size and preservation), and not grooved. The dorsal notum bears non-caryophyllidia tubercles: large tubercles being irregularly surrounded by smaller ones. The edge of the gill opening is smooth, as well as the margin of the rhinophoral sheaths. Small holes (diameter < 10 μm) and small tufts of cilia were observed on the mantle, although the notum was poorly preserved. There are six tetrapinnate branchial plumes arranged in circle around the anus. The rhinophores have about 35 lamellae.

Digestive system. The esophagus is long, large, and convoluted (with five or six tight loops). The internal surface of the esophagus is covered with conical papillae (up to 150 μm). The stomach is large, freely located on top of the left anterior side of the digestive gland. In this specimen, the digestive gland was exceptionally small with respect to the other digestive organs. A caecum is present but cannot be seen by dorsal dissection. The intestine is straight and dorsal. The labial cuticle is smooth. The radular sac cannot be seen by dorsal dissection. The length of the radula equals less than twice its width. The radular formula is 30 × (70-0-70) in a 75 mm long specimen. The rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the first third innermost teeth whose size increases gradually and the last ten outermost ones whose size decreases gradually. All teeth are hamate, including the outermost teeth. The teeth are not grooved, nor are they denticulate.

Nervous system. The length of the circumesophagal nerve ring equals approximately three times the width of the cerebro-pleural ganglia (*c.* 4 mm). All ganglia are fused. A few spherical structures can be seen by transparency through the dorsal membrane that protects the cerebro-pleural ganglia, which is probably due to the large size of the nervous system.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is loosely convoluted, almost straight. The division between male and female ducts (hidden within the female gland mass) could not be seen by dissection. The flattened prostate is divided in two parts. The deferent duct is highly coiled with multiple loops. It ends in a cavity that is equivalent to a penial sheath but that is actually empty. However, the distal end of the deferent duct, just before it reaches the penial sheath, which likely

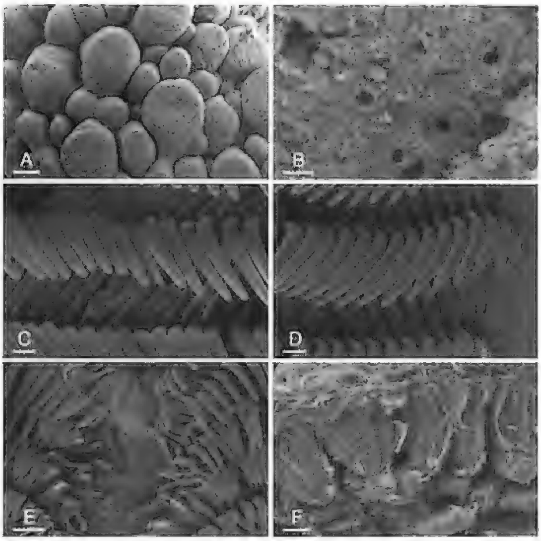

FIGURE 289. *Discodordidae lentiginosa*, CASIZ 168031. A. Dorsal notum, scale = 200 µm.— B. Dorsal notum, detail, scale = 10 µm.— C. Radula, median teeth, scale = 100 µm.— D. Radula, outermost teeth, scale = 100 µm.— E. Radula, innermost teeth, scale = 200 µm.— F. Internal, esophageal papillae scale = 40 µm.

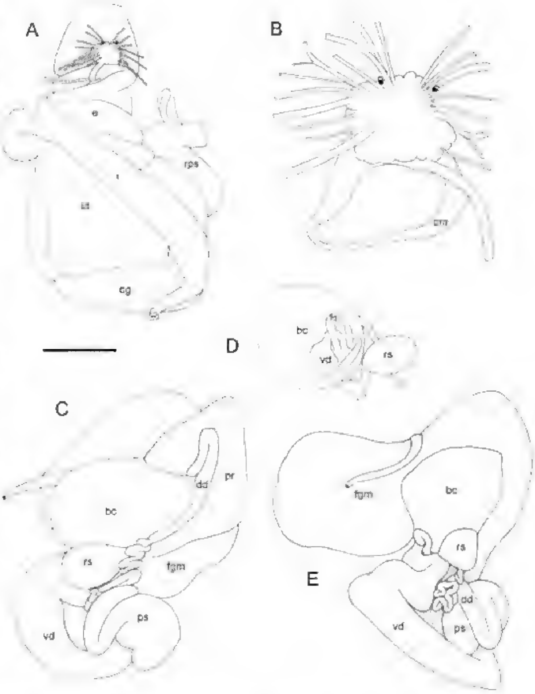

FIGURE 290. *Discodordidae lentiginosa*, CASIZ 168031. A. General anatomy, scale = 12 mm.— B. Nervous system, scale = 3 mm.— C. Reproductive system, scale = 5.5 mm.— D. Spermatic pouches, scale = 4 mm.— E. Reproductive system, scale = 5 mm.

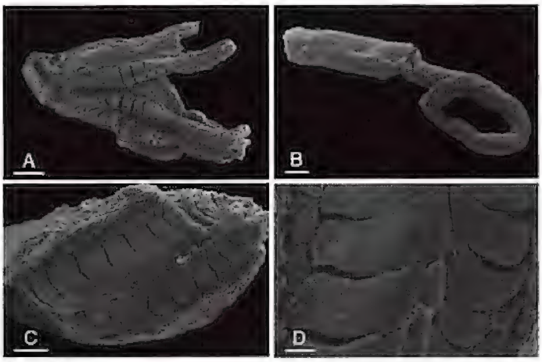

FIGURE 291. *Discodordidae lentiginosa*, penis, CASIZ 168031. A. Penial plate-like spines, scale = 200 µm.— B. Distal deferent duct with distal, penial plate-like spines, scale = 400 µm.— C. Penial plate-like spines, scale = 100 µm.— D. Penial plate-like spines, scale = 40 µm.

is evaginable, is covered with (four or five) longitudinal rows of strong, plate-like spines. The vaginal duct is broad and loosely convoluted. Its distal part is wide. The deferent duct and the vaginal duct join together and form a short vestibule not clearly separated from the female duct. The fertilization duct is convoluted (with a few loops). The connection between the fertilization duct and the female gland mass is marked by a distinct duct and could be observed. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is hidden by the receptaculum seminis and the vaginal duct. The bursa copulatrix is about six times larger than the receptaculum seminis. The bursa copulatrix and the receptaculum seminis, both ovate-spherical, are close to one another.

DIAGNOSTIC FEATURE.— As pointed out by Sandra Millen in the original description, the longitudinal rows of strong, plate-like spines in the distal portion of the deferent duct can hardly be mistaken. However, they are small (each row is approximately 100 µm wide and 0.5 mm long) and can only be observed in detail through SEM. Although the size and shape of the penial armature might vary among individuals, it is likely that its general characteristics will remain easily recognizable.

INFRA-SPECIFIC CHARACTER VARIATION.— Given that only two anatomical descriptions are available (the original description and the present study), the individual character variation can hardly be addressed. The maximum number of radular rows observed so far is 30, for 70 teeth per row, in a 75 mm long, preserved specimen (present study).

Discussion.— In the original description, Millen compared *lentiginosa* with a few other species, e.g., *Sebadoris nubilosa*. She rightly points out that *lentiginosa* could hardly be mistaken: its copulatory organ is distinct.

Supra-specific relationships.— A phylogenetic test of the relationships of *lentiginosa* shows that it does not belong to the clade *Peltodoris* and that it cannot be classified in *Anisodoris* because the latter is not a clade: *lentiginosa* is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial name for *lentiginosa* should thus be "*Montereina*" *lentiginosa*. Possible names under the *ICPN* are "*Montereina*" *lentiginosa* or simply *Discodorididae lentiginosa*.

"*Montereina*" *lippa* (Valdés, 2001) New combination
Discodorididae lippa (Valdés, 2001) New combination

Figure 292.

Peltodoris lippa Valdés, 2001:277-281, figs 29A, 30-31.

Type material.— Holotype (MNHN, no registration number), by original designation: one specimen 20/13 mm preserved, leg. Philippe Bouchet and Bertrand Richer de Forges [Musorstom 8 expedition], 11 October 1994.

Type locality.— Vanuatu, 15°38′S, 167°03′E, 161-182 meters depth, station CP 1132 of the Musorstom 8 expedition.

Type material condition.— Valdés dissected the holotype. No SEM stub is deposited at the MNHN (for the radula and the labial cuticle). The reproductive system was largely destroyed prior to the present study and is no longer informative.

Distribution.— The holotype is the only specimen known.

Remarks on the original description (Fig. 292).— Valdés described several general characters found in basal discodorids, such as the notched superior lip of the bilabiate anterior foot, and the conical oral tentacles. Based on field notes, the live animal was of a uniformly translucent white. According to Valdés's description, the tubercles on the dorsal notum are not caryophyllidia. However, as shown in one SEM picture (Valdés 2001: fig. 30D), the dorsal notum is not well preserved. The oral tentacles are not grooved. The radula and the smooth labial cuticle could not be re-examined because the SEM stubs prepared by Valdés were not deposited at the MNHN: the radular formula is 15 × (31-0-31); the outermost tooth bears denticles; based on one SEM picture from the original description (Valdés 2001: fig. 30A), the rachidian space seems to be narrow and the 10 innermost teeth are not much smaller than the rest of the teeth. No features could be verified for the reproductive system, largely destroyed and uniformative. Based on Valdés's description (2001: fig. 31B), the deferent duct is straight, with a loose loop, the vaginal duct is convoluted, with three tight loops. It is unclear whether the "unarmed penis" described by Valdés is a distinct, permanent penis, or just the evaginable distal part of the deferent duct.

Discussion.— Based on the color (translucent white) and its locality (deep waters off Vanuatu), this specimen may definitely be part of a distinct species. However, the anatomical features described by Valdés cannot be regarded as diagnostic of *lippa*, until we have access to more specimens and, through them, to the individual variation: e.g., the outermost teeth of the radula of *lippa* may lack denticles; the vaginal duct may be less convoluted. Also, the actual shape of the penis, which is a key taxonomic character, was not illustrated with SEM pictures. Note that the shape of the penis will always remain unknown because the penis is missing from the material.

SUPRA-SPECIFIC RELATIONSHIPS.— According to Valdés, *lippa* shares a number of features with *Peltodoris atromaculata*. This surely is correct. However, none of those features is diagnostic of *Peltodoris*. In other words, those features are symplesiomorphies of *Discodorididae*. Valdés overlooked an important difference between *atromaculata* and *lippa*, i.e., the size and shape of the ten innermost teeth. Valdés used an erroneous an erroneous (because non-phylogenetically based) diagnosis of *Peltodoris* to classify *lippa* within *Peltodoris*. A phylogenetic test of the position of *lippa* shows that it does not belong to the clade *Peltodoris*: it actually is part of the metaphyletic group at the base of *Discodorididae*. Therefore, the Linnaean name for lippa should be "*Montereina*" *lippa*. Possible names of *lippa* under the *ICPN* are "*Montereina*" *lippa* and *Discodorididae lippa*.

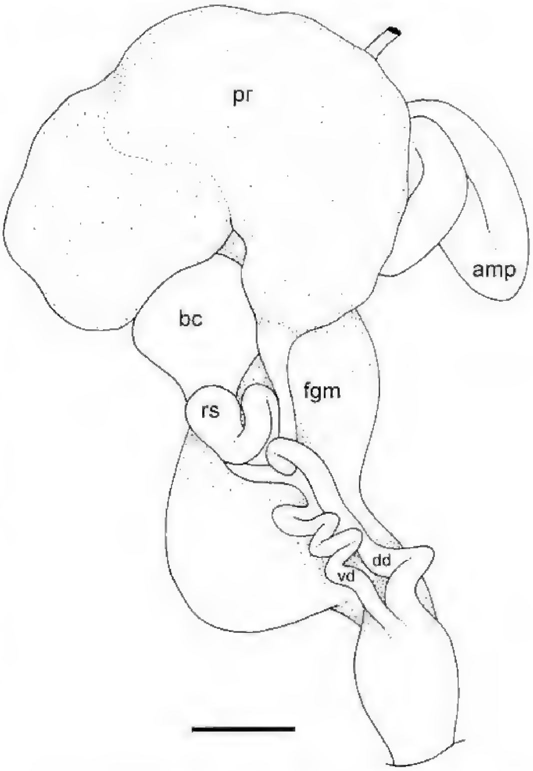

FIGURE 292. *Discodorididae lippa*, reproductive system, after Valdés (2001: fig. 31), scale = 0.5 mm.

"*Montereina*" *modesta* (Bergh, 1877) New combination
Discodorididae modesta (Bergh, 1877) New combination

Figure 293.

Discodoris modesta Bergh, 1877a:534-536, plate LIV, figs 21-25, plate LV, figs 17-19.— Eliot, 1910a:411, 423-424.

TYPE MATERIAL.— Holotype (ZMUC GAS-2129), by monotypy: one specimen 26/18 mm preserved, leg. Semper, 1861.

TYPE LOCALITY.— Aibukit, Philippines.

TYPE MATERIAL CONDITION.— The holotype was dissected by Bergh. Just the body wall remains in the jar. No slides could be found. A piece of digestive gland and some ducts (probably part of the reproductive system) are also in the jar, but a note by Kathe R. Jensen, who curated most of Bergh's collection at the ZMUC, indicates that those organs may not belong to the holotype of *modesta*. They are largely uninformative anyway.

DISTRIBUTION.— In addition to the type locality (Philippines), *modesta* was also mentioned in the Seychelles, Indian Ocean, by Eliot (1910a), although this record is doubtful because it is hard to know what *modesta* really is (see discussion). Note that Bergh (1884a) simply mentioned the name *modesta* in a list of *Discodoris* species, with no additional data.

REMARKS ON THE ORIGINAL DESCRIPTION (Fig. 293).— The preserved animal measures 26/18 mm. Its dorsal notum is homogeneously light brownish (it was described as yellowish by Bergh). There are no traces of blotches or dots. The dorsal tubercles are not caryophyllidia. The oral tentacles are digitiform. The foot is bilabiate anteriorly and the upper lip is notched. Bergh mentioned six branchial plumes and rhinophores with 50 lamellae. He found two sickle-shaped jaw plates and a radular formula of 29 × (48-0-48). The teeth are not denticulate and the outermost teeth are elongated. The description of the reproductive system is hardly informative: no copulatory organ was described.

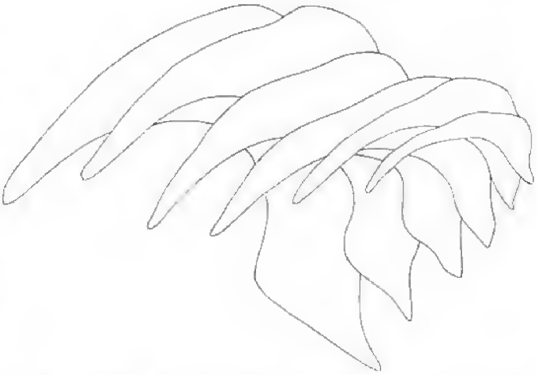

FIGURE 293. *Discodorididae modesta*, outermost teeth, after Bergh (1877a: plate LV, fig. 18).

DISCUSSION.— Here *modesta* is regarded as a *nomen dubium* because it is almost impossible to re-identify it based on Bergh's description. The examination of the type specimen does not help. It is unclear how Eliot (1910a) could identify a specimen from the Seychelles as *modesta*. Also, Eliot thought that *modesta* was "nearly allied" to *Discodoris cebuensis*. The shape of the tubercles of the holotype of *modesta* and Bergh's original description (especially the description of the radular teeth) do not support this synonymy. Eliot probably misidentified *Discodoris cebuensis* (see this species).

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *modesta* shows that it does not belong to the clade *Discodoris*: it is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial name for *modesta* should thus be "*Montereina*" *modesta.* Possible names under the *ICPN* are "*Montereina*" *modesta* or simply *Discodorididae modesta*.

"*Montereina*" *mortenseni* (Marcus & Marcus, 1963) New combination
Discodorididae mortenseni (Marcus & Marcus, 1963) New combination

Figures 294-303.

Discodoris mortenseni Marcus and Marcus, 1963:30-32, figs 36-39.— Marcus and Marcus, 1970a:65, fig. 116.— Marcus, 1972:296.— Hess and Abbott, 1994:164.— Bertsch, 1975:416-417, fig. 1.

TYPE MATERIAL.— Holotype (ZMA Moll. 3.63.022), by original designation: one specimen 12/9 mm preserved, leg. Dr. Diva Corrêa, 3 June 1962. Paratype (ZMA Moll 3.63.023): one specimen ~9/7 mm preserved, leg. Th. Mortensen, April 1916. We learn from the original description that the holotype was sent to Dr. Hummelinck, Utrecht. The specimen received as 'holotype' was not specifically labeled as being the holotype. Therefore, it is not certain that the specimen ZMA Moll. 3.63.022 is the actual holotype. Also, Eveline and Ernst Marcus do not indicate exactly how many specimens they designated as paratypes. The label of the specimen ZMA Moll 3.63.023 was received with the mention 'paratype' written on it. It cannot be excluded that additional paratypes will be found in the Marcus' collection, at the MZSP (although no *mortenseni* material has been found there so far; pers. com. Dr. Luiz Simone): the original description tells us that a radula of a paratype was kept in São Paulo.

TYPE LOCALITY.— Piscadeira Baai, Curaçao, Caribbean Sea. The paratype was collected from a coral reef in Tobago, Caribbean Sea.

TYPE MATERIAL CONDITION.— The holotype is entire. However, it is in poor condition: it probably dried for a while and then was transferred again into alcohol (the original description indicates that the largest specimen was dry, but it is unclear whether or not it is the holotype re-examined here). Except for the radula that might be extracted, It seems that it will never provide any valuable information. Its color is typical of dry specimens, i.e., dirty creamish. The paratype was dissected by Eveline and Ernst Marcus: it dried too, and is completely destroyed, consisting of a dark brown piece of the digestive gland and a small piece of notum. A piece of notum was prepared for both types. Also, the buccal mass and the reproductive system (that could not be separated) were taken out of the body cavity of the holotype in order to check some features in the reproductive system. However, this was not fruitful because the latter was so poorly preserved that no observations could be made.

ADDITIONAL MATERIAL DISSECTED.— **Caribbean Sea**, Florida, Florida Keys, Key West, August 1990, one specimen 9/4 mm preserved, leg. T. M. Gosliner, identified as *Discodoris mortenseni* by T. M. Gosliner (CASIZ 074398) [specimen dissected by T. M. Gosliner, who took some SEM pictures of the radula; reproductive system missing]; Cayman Islands, Grand Cayman Island, S. of West Bay, near Soto's Reef, Burger King Reef, on shallow reef, 8 May 1991, four specimens 24/13 (#1), 19/10 (#2), 14/8 (#3), 11/7 (#4), and 10/6 (#5) mm preserved, leg. T. M. Gosliner, identified as *Discodoris mortenseni* by T. M. Gosliner (CASIZ 077292); Mexico, Yucatan Peninsula, Quintana Roo, Cozumel, Paradise Reef, 24 March 1985, two specimens 10/4 (#1) and 9/4 (#2) mm preserved, leg. T. M. Gosliner, identified as *Discodoris mortenseni* by T. M. Gosliner (CASIZ 074656).

ADDITIONAL MATERIAL EXAMINED (*IDENTIFICATION UNCERTAIN*).— **Caribbean Sea**, Belize, Glover's reef, NE Cay, 17 August 1973, one specimen 10/7 mm preserved, leg. R. S. Houbrick, identified as *Discodoris mortenseni* probably by R. S. Houbrick (USNM 820894) [this specimen was entirely dissected prior to the present study: the radula and the reproductive system were missing, so the identification could not be verified].

DISTRIBUTION.— Caribbean Sea. So far, *mortenseni* was recorded from Curaçao (type locality; Marcus and Marcus 1963, 1970a), Tobago (Marcus and Marcus 1963), Puerto Rico (Marcus and Marcus 1970a), Florida (Marcus 1972; present study), Cayman Islands (Hess and Abbott 1994; present study), Caribbean coast of Panama (Bertsch 1975). Note, however, that several identifications (Marcus 1972; Bertsch 1975; Hess and Abbott 1994) were not demonstrated with internal, diagnostic features, and should probably not be taken for granted. Finally, *mortenseni* might be present in Belize (USNM 820894; present study), which is not surprising based on its known distribution.

OCCURRENCE.— Less than ten specimens have been mentioned in the literature or deposited in museum collections (most of which in Curaçao).

HABITAT.— Under stones in shallow water (Marcus and Marcus 1963, 1970a; Bertsch 1975), on sand (Marcus and Marcus 1963), feeding on sponges (Hess and Abbott 1994).

LITERATURE.— The anatomical and morphological data available in the literature are rare: two drawings of radular teeth (Marcus and Marcus 1963, 1970a), a drawing of a penial papilla (Marcus and Marcus 1963) and an uninformative representation of the reproductive system (Bertsch 1975). No color picture was published prior to the present study.

REMARKS ON THE ORIGINAL DESCRIPTION (Figs. 295, 298A-C).— Eveline and Ernst Marcus described a notum "stiffened with spicules" and bearing "spiculate papillae." The latter description and the drawing published by Marcus and Marcus (1963:68, fig. 37) suggest that those notal papillae are cayophyllidia. However, the notum of both types is currently destroyed and even SEM pictures could not positively demonstrate the presence of caryophyllidia. The color of the live animal was described as "pinkish with light-brown spots and white specks on the notum and dark gills." The types are currently colorless (because they both dried) The oral tentacles are digitiform and not grooved. The upper lip of the bilabiate, anterior foot is notched. Marcus and Marcus mention six branchial plumes: they could hardly be counted, but the number is either five or six. Eveline and Ernst Marcus mention 20 rhinophoral lamellae: They could not be counted. The labial cuticle is armed with jaw plates. The radular formulae are: 14 × (32-0-32) in a 20 mm long, live animal (Curaçao) and 22 × (39-0-39) in the ~9 mm long, preserved specimen from Tobago (paratype).

More importantly, they described and illustrated the denticulation of both the penultimate tooth and the outermost tooth. The penial papilla bears "a few minute cuticular hooks" (size not indicated). Given the sizes of the (smooth) papillae obtained here (about 0.1 mm), one can wonder whether the Marcus really saw some hooks or some artifacts, although hooks could have missed Here too. Apart from the penial papilla, the description of the reproductive system is not helpful. The observation of the reproductive system of the holotype was less exciting than expected because (due to poor preservation) no organs could be identified. However, a few convoluted ducts (probably the deferent duct and the fertilization duct) are fully compatible with was observed in non-type specimens.

Description of new specimens (Figs. 294, 296-303).— *Color*. The dorsal notum of the live animal from the Cayman Islands (CASIZ 077292) was whitish-creamish, bearing darker, light reddish blotches of irregular sizes and arranged all over the dorsal notum. A few white dots can be seen, especially on the gills and rhinophores. The animal looks pinkish though. Preserved, this specimen is homogeneously whitish, on the ventral and the dorsal surfaces. All other preserved specimens are also whitish or creamish.

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform but not grooved. The nature of the dorsal tubercles (absence *vs.* presence of caryophyllidia) is problematic. The notum was not well preserved and even SEM pictures did not help; however, a specimen with a well-preserved notum does not seem to bear caryophyllidia, which suggests that caryophyllidia might be absent. Many small holes (diameter < 10 µm) and many small tufts of cilia are present on the surface of the mantle, including the tubercles, the gills, and the rhinophores. In preserved specimens, the margins of the rhinophoral

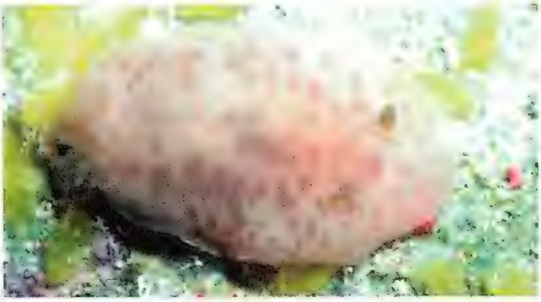

FIGURE 294. *Discodorididae mortenseni*, dorsal color, CASIZ 077292 (one of five specimens) (T.M. Gosliner).

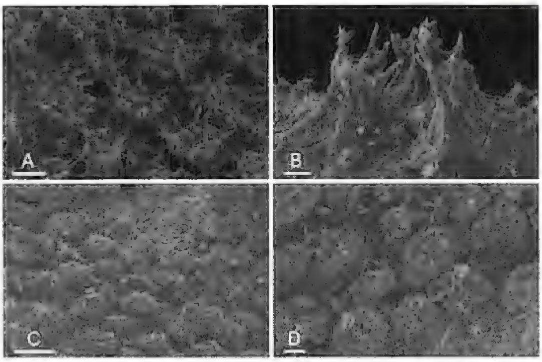

FIGURE 295. *Discodorididae mortenseni*, notum, types. A. Holotype, scale = 100 µm.— B. Holotype, scale = 40 µm.— C. Paratype, scale = 100 µm.— D. Paratype, scale = 30 µm.

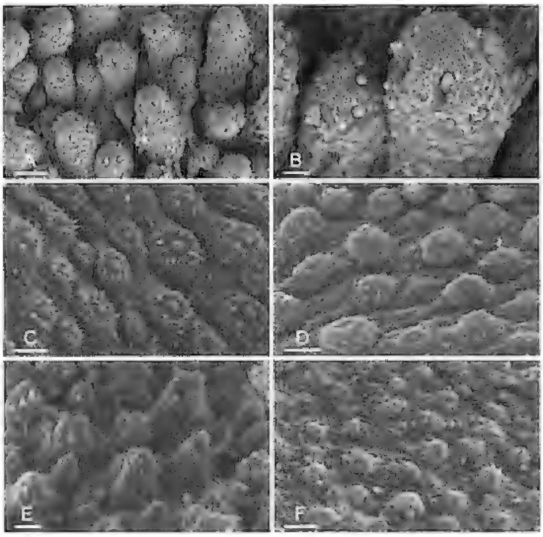

FIGURE 296. *Discodorididae mortenseni* dorsal notum, tubercles. A. CASIZ 077292 (#1), scale = 100 µm.— B. CASIZ 077292 (#1), scale = 20 µm.— C. CASIZ 077292 (#3), scale = 100 µm.— D. CASIZ 077292 (#4), scale = 100 µm.— E. CASIZ 074398, scale = 20 µm.— F. CASIZ 074656 (#2), scale = 100 µm.

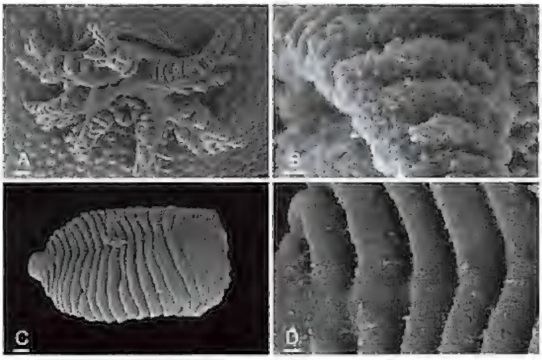

FIGURE 297. *Discodorididae mortenseni*, rhinophores and gills. A. Branchial plumes and anus, CASIZ 077292 (#3), scale = 200 µm.— B. Branchial plume, detail, CASIZ 077292 (#3), scale = 20 µm.— C. Rhinophore, CASIZ 077292 (#1), scale = 100 µm.— D. Rhinophoral lamellae, detail, CASIZ 077292 (#1), scale = 20 µm.

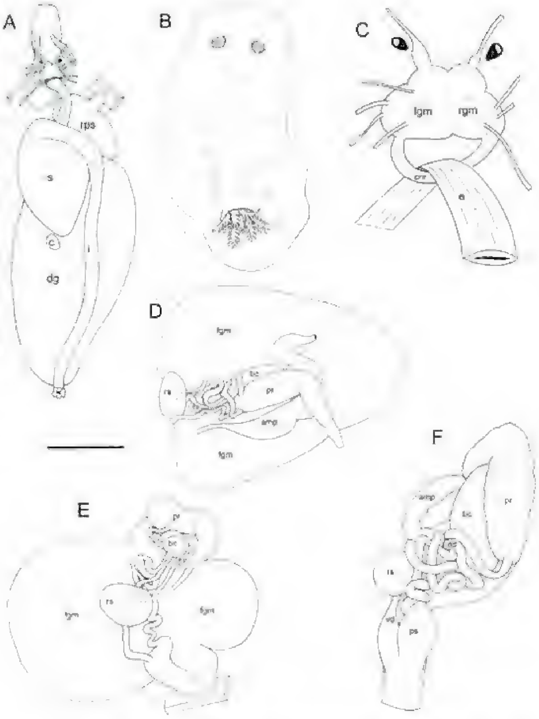

FIGURE 299. *Discodorididae mortenseni*, CASIZ 077292 (specimen # 1, except F). A. General anatomy, scale = 3.7 mm.— B. Dorsal view (as currently preserved), total length = 24 mm.— C. Nervous system, scale = 0.7 mm.— D. Reproductive system (prostate 1 moved on the side), dorsal view, scale = 1.3 mm.— E. Reproductive system, lateral view, scale = 1.3 mm.— F. Reproductive system, specimen #5, scale = 0.6 mm.

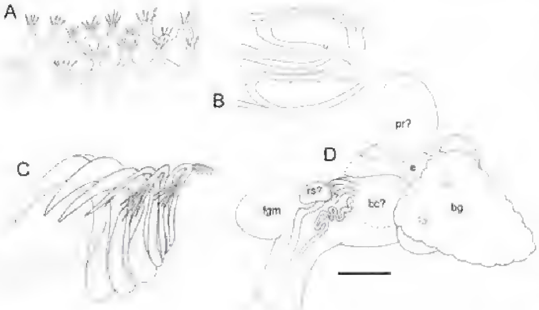

FIGURE 298. *Discodorididae mortenseni*. A. Dorsal notum, after Marcus and Marcus (1963: fig. 37).— B. Penial papilla, after Marcus and Marcus (1963: fig. 39).— C. Outermost teeth, after Marcus and Marcus (1970a: fig. 116).— D. General, anterior anatomy of the holotype as currently preserved (reproductive system, buccal mass covered by blood gland), the identification of structures tentative because dry, poorly preserved specimen, scale = 0.5 mm.

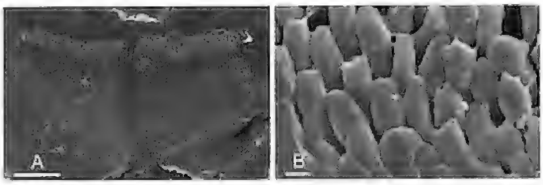

FIGURE 300. *Discodorididae mortenseni*, CASIZ 077292 (#1), jaws. A. Labial cuticle, scale = 100 µm.— B. Rodlet elements, scale = 4 µm.

sheaths can be smooth or lightly crenulate. There are six tripinnate branchial plumes arranged in circle around the anus. The rhinophores have up to 20 lamellae, depending on the size of the animal.

Digestive system. The stomach is free, on top of the left, anterior side of the digestive gland, on the left. A small caecum is located on the left-posterior side of the stomach. The intestine is straight and dorsal. The labial cuticle is armed with two sickle-shaped jaw plates that consist of rodlets. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. Radular formulae are: 20 × (30-0-30) in a 24 mm long specimen (CASIZ 077292 #1), 18 × (27-0-27) in a 14 mm long specimen (CASIZ 077292 #3), 10 × (24-0-24) in a 10 mm long specimen (CASIZ 077292 #5), 14 × (34-0-34) in a 9 mm long specimen (CASIZ 074656 #2), and 11 × (21-0-21) in a 9 mm long specimen (CASIZ 074398). Rachidian teeth are absent. The rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis.

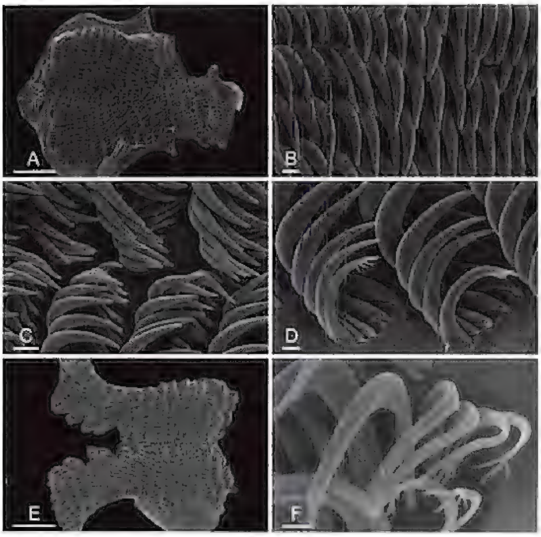

FIGURE 301. *Discodorididae mortenseni* radula. A. Radula, CASIZ 077292 (#1), scale = 300 µm.— B. Median teeth, CASIZ 077292 (#1), scale = 20 µm.— C. Innermost teeth, CASIZ 077292 (#1), scale = 20 µm.— D. Outermost teeth, CASIZ 077292 (#1), scale = 10 µm.— E. Radula, CASIZ 077292 (#3), scale = 200 µm.— F. Outermost teeth, CASIZ 077292 (#3), scale = 10 µm.

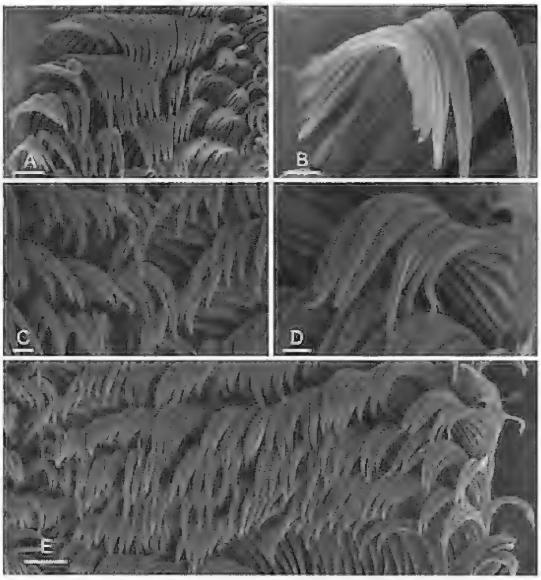

FIGURE 302. *Discodorididae mortenseni* radula. A. Left rows, CASIZ 077292 (#5), scale = 30 µm.— B. Outermost teeth, CASIZ 077292 (#5), scale = 10 µm.— C. Innermost teeth, CASIZ 077292 (#2), scale = 10 µm.— D. Outermost teeth, CASIZ 077292 (#2), scale = 10 µm.— E. Right rows, CASIZ 077292 (#2), scale = 40 µm.

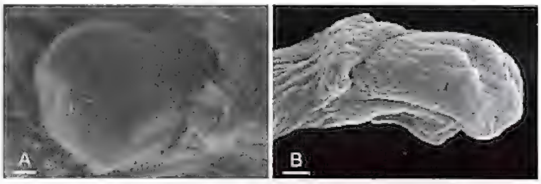

FIGURE 303. *Discodorididae mortenseni*, penis. A. CASIZ 077292 (#5), scale = 20 µm.— B. CASIZ 077292 (#1), scale = 20 µm.

The size increases gradually towards the middle of the radula, then remains more or less stable, and then decreases towards the outermost teeth. The last outermost tooth may be reduced. The last outermost teeth bear a few denticles. The number of denticulate outermost teeth varies from one to three (most often three).

Nervous system. The length of the circum-esophageal nerve ring equals less than twice the width of the cerebro-pleural ganglia. The ganglia are fused. Their surface is smooth.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is convoluted. The division between male and female ducts, within the female gland mass, could not be seen by dissection. The prostate is divided in a proximal part and a distal part. The deferent duct is convoluted: its first, tight, proximal loop is on the surface of the bursa copulatrix. In a small specimen (CASIZ 077292 #5) with an immature reproductive system (with a reduced female gland mass), the deferent duct appeared to be long and much more convoluted than in fully mature specimens. This was found in several species, probably because the deferent duct develops first and then uncoils when the female gland mass grows. The copulatory organ is small (up to 0.14 mm in length) and could definitely be the evaginable part of the deferent duct. In any case, it is unarmed. The vaginal duct is straight loosely convoluted. The fertilization duct is convoluted (with two or three tight loops). The connection between the fertilization duct and the female gland mass is marked by a short duct. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is underneath the receptaculum seminis. The size of the bursa copulatrix equals about three times the size of the receptaculum seminis. Both spermatic pouches are spherical-ovate; the bursa copulatrix may be embedded with the prostate.

Diagnostic features.— It is difficult to propose clear-cut diagnostic features for *mortenseni* at this stage. The color variation is still poorly known, and *mortenseni* could easily be confused with other species such as *Discodorididae branneri* or *Tayuva lilacina* (so far referred to as *hummelincki* in the Caribbean), although it is true that these two species do not look pinkish. A few internal features could be useful: the organization of the reproductive system, especially the loops of the deferent duct; the denticulate outermost teeth (although denticulation in outermost teeth is actually common in discodorids). Also, note that this denticulation varies infra-specifically.

Infra-specific character variation.— There is not much to add to the description above. The largest animals known are a 33 mm long specimen from Panama (Bertsch 1975), a 28 mm long specimen from Puerto Rico (Marcus and Marcus 1970a) and a 24 mm long, preserved specimen (present study). The dorsal notum of live animals was described as pinkish or grayish pink (Marcus and Marcus 1970a). The radular formulae described here fit well within the radulae described in the literature. In addition to the original description, radular formulae are: 18 × (35-0-35) in a 12.5 mm long, preserved specimen (Marcus and Marcus 1970a), 16 × (20-0-20) in a 6 mm long, preserved specimen (Marcus and Marcus 1970a), and 14/16 × (22/29-0-22/29) in a 33 mm long, live animal (Bertsch 1975).

Discussion.— The taxonomy of *mortenseni* is problematic for several reasons. First, it was not possible to determine with certainty whether or not the dorsal notum of *mortenseni* bears caryophyllidia. SEM pictures of the notum of the types did not solve the problem: the notum is destroyed and it is hard to make any decision. Marcus and Marcus (1963, 1970a) have mentioned twice a penial papilla with spines. No spines could be found even with SEM pictures. Finally, the reproductive system of the type specimens (not illustrated in the original description) is currently largely uninformative, and it could not be determined whether or not it is the same as that of the non-type specimens described here. Now, the long, slender denticles of the outermost teeth are quite distinctive, and they could help recognize *mortenseni* (although one must be cautious because similar denticles can be found in other species). Finally, note that a few specimens from the Galapagos are described here as a potentially new species and closely related to *mortenseni* (see sp. D).

Supra-specific relationships.— A phylogenetic test of the relationships of *mortenseni* shows that it does not belong to the clade *Discodoris*: it is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial name for *mortenseni* should thus be "*Montereina*" *mortenseni*. Possible names under the *ICPN* are "*Montereina*" *mortenseni* or simply *Discodorididae mortenseni*.

"*Montereina*" *muta* (Bergh, 1877) New combination
Discodorididae muta (Bergh, 1877) New combination

Figures 304-305.

Discodoris muta Bergh, 1877a:532-534, plate LXII, figs 15-20.— Bergh, 1884a:93.— Eliot, 1906e:131, 137-139.

Type material.— Two syntypes (ZMUC GAS-2128): two specimens 28/11 (#1) and 22/15 (#2) mm preserved, leg. Mr. G. Schramm, [no collecting date], [these two specimens were identified as *Doris crucis* by Mörch in 1869].

Type locality.— Guadeloupe, Caribbean Sea.

Type material condition.— One syntype (#1) was entirely dissected by Bergh who left only the empty body wall in the jar. The other one (#2), entire, was dissected for the present study.

However, the organs were poorly preserved and the tissues were extremely fragile. The digestive gland, instead of being hard would break in multiple pieces as soon as it would be touched. The reproductive system could be described without breaking it, but was fragile: several organs were difficult to identify.

DISTRIBUTION.— Guadeloupe (type locality of *muta*); the presence of '*muta*' in the Cape Verde Islands (Eliot, 1906e) is questionable (see discussion).

OCCURENCE.— So far, *muta* is only known from the two syntypes. An additional specimen was identified by Eliot (1906e) as *muta*, but this identification could not be verified.

LITERATURE.— Bergh (1884a) briefly mentioned *muta* in a checklist of *Discodoris* species. Marcus and Marcus (1967a) briefly mentioned *muta* in a list of *Discodoris* species. They thought that Bergh's description of innermost teeth with a split base was probably characteristic of this species. Ballesteros et al. (1985) briefly proposed that the specimens identified as *muta* by Eliot from the Cape Verde Islands were specimens of *Discodoris confusa*, i.e., *Tayuva lilacina* (see this species). The authors, however, argued that a re-description of *muta* from the Caribbean Sea was necessary.

REMARKS ON THE ORIGINAL DESCRIPTION (Figs. 304-305).— The color of the live animal is unknown. Currently, one syntype (#1) is homogeneously whitish. The other one (#2) is creamish with a few traces of darker blotches on the dorsal notum. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two digitiform, oral tentacles are not grooved. The dorsal notum bears tubercles that are not caryophyllidia (although the notum is poorly preserved and the tubercles are hardly distinguishable). Acceding to Bergh, there are six tripinnate branchial plumes arranged in circle around the anus: they are poorly preserved in syntype #2. The rhinophores have up to 30 lamellae. The stomach is free, on top of the digestive gland, on the left. A small caecum is located on the left-posterior side of the stomach. The intestine is dorsal; it is slightly bent on the right, but remains dorsal. The labial cuticle is armed with a pair of jaw plates. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. Radular formulae are: 26 × (41-0-41) in a 28 mm long specimen (syntype #1, Bergh's dissection), 16 × (34-0-34) in a 22 mm long specimen (syntype #2, dissection for the present study). Rachidian teeth are absent and rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the first ten innermost teeth increases gradually for about one third of the row, then remains more or less constant, and then decreases for the last five outermost teeth. The last outermost tooth may have a reduced base. Also, the last outermost tooth is smooth, i.e., with no denticle (Bergh's description), or it can bear one or two short denticles (syntype #2, dissection for the present study). Those denticles are not present in all rows though. Bergh's description of a split base for the innermost teeth is unclear to me. This split base was not found in the radula of syntype #2. However, interestingly, some innermost teeth were close to each other, and, as a result seemed to be one tooth with a split base. It is possible that Bergh, without SEM, could only see one tooth instead of two. The length of the circum-esophageal nerve ring equals about twice the width of the two cerebro-pleural ganglia. The cerebral and pleural ganglia are fused, and are loosely separated from the pedal ganglia. The surface of the ganglia is smooth. The reproductive system, briefly and incompletely described by Bergh, is located on the right side of the body, between the buccal mass and the digestive gland. Here follows the description of the reproductive system of syntype #2. The ampulla is convoluted (one loop). The division between male and female ducts, within the female gland mass, could not be seen by dissection. The prostate is poorly preserved and it is unclear whether it is divided in two parts or not. The deferent duct is straight. Also, whether its proximal part (which is not wide) was folded internally or not, as in could not be established. The penis is a simple papilla, 0.3 mm long. The vaginal duct is straight. The fertilization duct is tightly convoluted with two tight loops near the bursa. The connection between the fertilization duct and the female gland mass could not be observed. The size of the (ovate) bursa copulatrix equals about four times the size of the (spherical) receptaculum seminis. Finally, the distal part of the reproductive system is surrounded by a piece of fragile tissue that could be identified as a piece of a muscular wall, as in *Tayuva*.

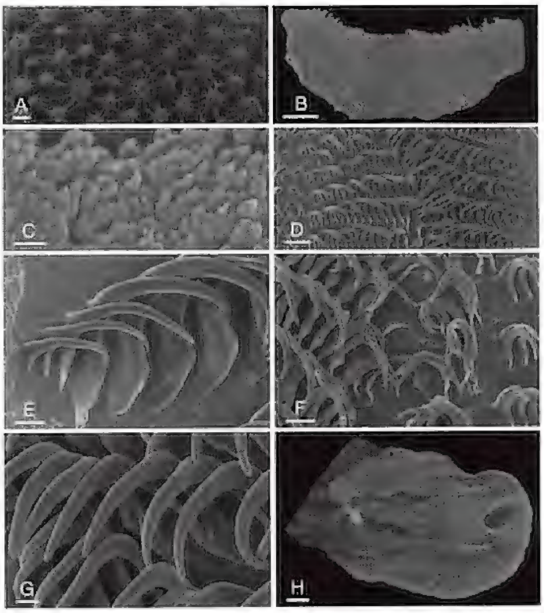

FIGURE 304. *Discodorididae muta*, syntype. A. Dorsal notum, tubercles, scale = 100 µm.— B. Jaws, scale = 100 µm.— C. Jaw rodlets, scale = 10 µm.— D. Radular rows, scale = 100µm.— E. Outermost teeth, scale = 10 µm.— F. Innermost teeth, scale = 20 µm.— G. Median teeth, scale = 20 µm.— H. Penis, scale = 20 µm.

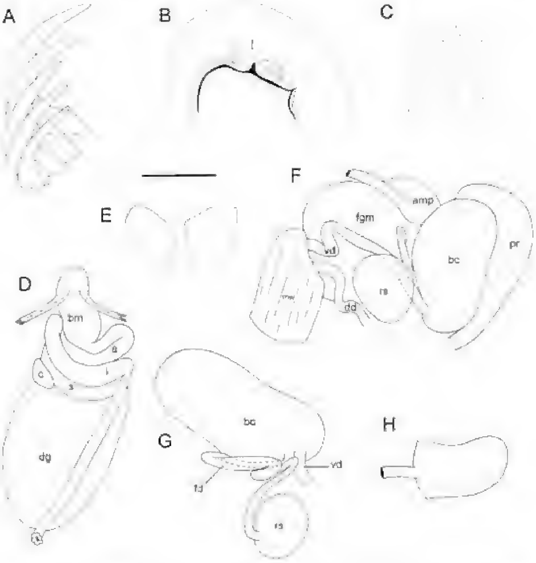

FIGURE 305. *Discodorididae muta*, syntype. A. Outermost teeth, after Bergh (1877a: LXII, fig. 18).— B. Anterior, ventral view, scale = 5 mm.— C. Dorsal pigmentation, scale = 1.3 mm.— D. General anatomy, scale = 5 mm.— E. Jaws, scale = 0.5 mm.— F. Reproductive system, scale = 1.2 mm.— G. Spermatic pouches and ducts, scale = 1 mm.

DISCUSSION.— It certainly is difficult to re-identify *muta* based on Bergh's description. Unfortunately, the re-examination of the type material and the redescription of a syntype (#2) do not help much. The main problem is the anatomy of the reproductive system of syntype #2, which was too poorly preserved to be adequately described: The proximal part of the deferent duct could not be checked carefully; a distal muscular wall seems to exist, but is weak and uncertain. Based on this, it is not possible to place *muta* in *Tayuva* (*muta* could have been a valid name for *Tayuva lilacina* (traditionally referred to as *hummelincki* in the Caribbean). This nomenclatural decision, however, is also weakened by the fact that the penis of *muta* differs from that of *lilacina* (even though some variation exists in the latter species). As a result, *muta* is regarded as a *nomen dubium*, because it is difficult to say what it designates, and new collections from the Caribbean may not solve this problem. Finally, Eliot (1906e) described a specimen from the Cape Verde Islands as *muta* because its anatomy "seems to agree in its principal internal and external features with *Discodoris muta*, Bergh, recorded from Guadaloupe." Both Bergh's and Eliot's descriptions are quite general and are compatible with quite a few discodorid species. Given that the re-examination of the type material did not help determine what *muta* is, it is unclear how Eliot could identify a sea slug as *muta*. At this stage, it is difficult to propose a species name for Eliot's specimen from the Cape Verde Islands. It could belong to *Tayuva*, as suggested by Ballesteros et al. (1985), who tentatively re-identified it as *Discodoris confusa*, i.e., *Tayuva lilacina* (formerly as *maculosa* from eastern Atlantic). However, it could be something completely different.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *muta* shows that *muta* does not belong to the clade *Discodoris*, but rather is part of a large metaphyletic group of species at the base of *Discodorididae*. So, *muta* can only be placed in "*Montereina*." The Linnaean binomial of *muta* should be "*Montereina*" *muta*. Possible names under the *ICPN* are "*Montereina*" *muta* or simply *Discodorididae muta*.

"*Montereina*" *nobilis* MacFarland, 1905
Discodorididae nobilis (MacFarland, 1905)

Figures 306-308.

Montereina nobilis MacFarland, 1905:38-39.
Anisodoris nobilis.— MacFarland, 1906:116-118, plate 18, figs 6-11, plate 22, figs 1-2.— MacFarland, 1966:188-190, plate 28, figs 1-3, plate 29, figs 16-17, plate 37, figs 22-27.— McDonald, 1983:145-146.
Archidoris nobilis.— Michel, 1976:46, fig. 3.
Peltodoris nobilis.— Valdés, 2002:586-591, figs 4I, 30-31.— Behrens and Hermosillo, 2005:75, fig. 144.
Discodorididae nobilis.— Dayrat and Gosliner, 2005:205.

TYPE MATERIAL.— Holotype (NMNH 181284), by original designation: leg. F. M. MacFarland. Not examined.

TYPE LOCALITY.— Monterey Bay, California.

ADDITIONAL MATERIAL DISSECTED.— California, Monterey Bay, Monterey County, Pacific Grove, March 1967, three specimens 45/30 (#1), 40/35 (#2), and 28/17 (#3) mm preserved, leg. A. Cameron, identified as *Anisodoris nobilis* by John Pearse et al., CASIZ 007098; California, Monterey County, off Pont Sur, 36°16.21′N, 121°57.09′W, 16 September 1988, one specimen 20/17 mm preserved, leg. T. M. Gosliner, identified as *Anisodoris nobilis* by T. M. Gosliner, CASIZ 087212.

DISTRIBUTION.— Northeastern Pacific: from Alaska to Ensenada (McDonald 1983; Berhens and Hermosillo 2005).

OCCURENCE.— It is a common species in rocky intertidal and subtidal zones (McDonald 1983).

HABITAT.— Rocky shore, occasionally on docks and pilings in bays. Feeds on sponges, such as *Halichondria*, *Haliclona*, and *Lissodendryx* (McDonald 1983). Found up to 250 meters depth (McDonald 1983).

LITERATURE.— The literature on *nobilis* is abundant: It is a common species, and many authors recorded its presence (McDonald 1983). The infra-specific variation of several features, such as the dorsal color and the radular formula, is well known. MacFarland (1906, 1966) published two thorough anatomical descriptions.

REMARKS ON THE ORIGINAL DESCRIPTION (Fig. 306).— The original description was based on multiple specimens, although MacFarland does not give any precise number. MacFarland mentions a 200 mm maximum length, for live animals, which is what is still cited in the literature. The body is "very large, plump, arched, but little depressed." The dorsal color is light yellow to rich orange-yellow for the background, "mottled everywhere between the tubercles with irregular blotches of dark brown or black, the total amount of dark coloration varying between wide limits in different individuals." The dorsal notum is "thickly tuberculate." The apex of tubercles end to be rounded. The six tri- or quadri-pinnate branchial plumes are "pinkish, tipped with white." There are about 24 rhinophoral lamellae. The foot is rounded at both anterior and posterior ends. The anterior foot is bilabiate, with the upper lip notched. The oral tentacles are digitiform or "bluntly conical." They are not grooved. The radular formula is 26 × (55/62-0-55/62). The rachidian space is "very narrow." MacFarland does not mention any tooth denticles. For the reproductive system, MacFarland mentioned the few characteristics (not diagnostic though) of *nobilis*, i.e., long deferent duct, unarmed "glans penis" and vagina.

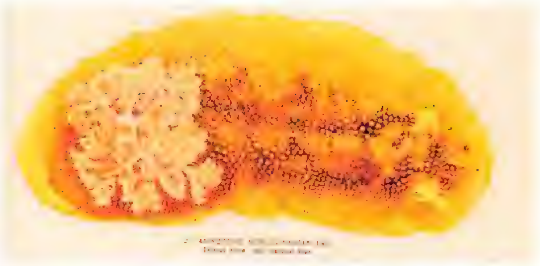

FIGURE 306. *Discodorididae nobilis*, dorsal view (MacFarland 1906: plate XXII, fig. 2).

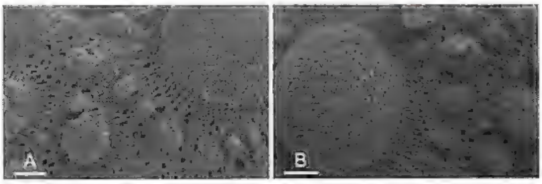

FIGURE 307. *Discodorididae nobilis*, dorsal notum, tubercles. A. CASIZ 087212, scale = 200 µm.— B. CASIZ 087212, scale = 200 µm.

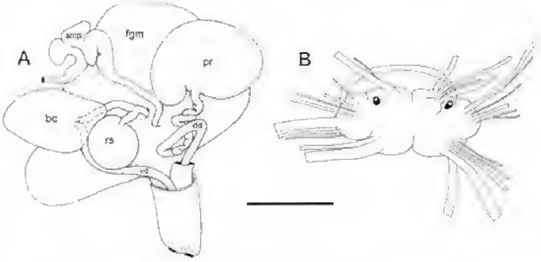

FIGURE 308. *Discodorididae nobilis*, CASIZ 007098 (#1). A. Reproductive system, scale = 4 mm.— B. Nervous system, scale = 2 mm.

DESCRIPTION OF NEW SPECIMENS (Figs. 307-308).— *Color*. No data on the live color was available for of the animals dissected here. However, the infra-specific variation of the color of *nobilis* is well known. Preserved specimens have a whitish-yellowish dorsal notum, with a few traces or dark blotches.

External morphology. The body is oval. Its length equals less than twice its width. The foot is rounded posteriorly and anteriorly. The width of the foot equals about one half of the width of the dorsal notum. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, not grooved. The dorsal notum is covered with the large rounded tubercles, which are quite different from the pointed, conical, tubercles found in species such as *Sebadoris fragilis*, *Peltodoris atromaculata*, or *Tayuva lilacina*. In preserved specimens, the margins of the rhinophoral and branchial sheaths can be smooth or crenulate. The margin of the gill opening is not star-shaped with five lobes. There are six wide multipinnate branchial plumes arranged in circle around the anus. The rhinophores have from 20 to 25 lamellae.

Digestive system. The stomach is large, free, on top of left, anterior digestive gland. A caecum is located on the left posterior side of the stomach. The labial cuticle is smooth. The radular sac cannot be seen by dorsal dissection. The radula formula is 18 × (48-0-48) in a 45 mm long specimen (CASIZ 007098 #1), 20 × (45-0-45) in a 40 mm long specimen (CASIZ 007098 #2). The rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the ten innermost teeth of which the size increases gradually and the last four to six outermost ones of which the size decreases gradually. All teeth are hamate, including the outermost ones. The teeth bear no denticle. However, in several rows (not all), there was a sharp outer denticle on the hook of the two first innermost teeth.

Nervous system. The circum-esophageal nerve ring is short: its length slightly higher than the width of the cerebro-pleural ganglia. The cerebral, pleural, and pedal ganglia can be distinguished in the dorsal nervous mass.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is convoluted, with several loops. The division between male and female ducts (in the female gland mass) could not be seen by dissection. The prostate is divided in a proximal whitish part and a distal yellowish part. The deferent duct is very long, convoluted, with many tight loops. The deferent duct ends in a small, conical, unarmed penial papilla. The vaginal duct is almost straight, or loosely convoluted. The fertilization duct is also straight. The connection between the fertilization duct and the female gland mass is marked by a clear duct. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is underneath the receptaculum seminis and the long, deferent duct. The bursa copulatrix is up to five times larger than the receptaculum seminis. Both pouches are spherical-ovate, with a smooth surface.

DIAGNOSTIC FEATURES.— The best way to identify *nobilis* clearly is its dorsal color. The black blotches remain on the background, i.e., never cover the tubercles, whereas, *Archidoris montereyensis* (Cooper, 1863), with which it is occasionally confused, has a light yellow dorsal background with black spots that can cover the tubercles (and, in any case, *montereyensis* does not have digitiform oral tentacles). Internal features are more problematic because many species have a long deferent duct, and the latter can hardly be regarded as diagnostic of *nobilis*. Finally, the peculiar, sharp outer denticle of the hook of the one or two innermost teeth seems to only be present in *nobilis*, but its presence varies among specimens.

INFRA-SPECIFIC CHARACTER VARIATION.— The individual variation originally described by MacFarland is still accepted today. All radular formulae found in the literature fit within this range of variation: 20/27 × (40/62-0-40/62) (McDonald 1983). A slightly smaller number of rows (18) was found, which is probably due to the fact that smaller individuals were intentionally dissected to look at variation of the radula and deferent duct. The latter is also well developed, long, tightly convoluted in the specimens dissected here. Those specimens were fully mature though. The deferent duct is long early in the development of the reproductive system, because the male parts probably develop first.

DISCUSSION.— The taxonomy of *nobilis*, as a species, seems to be straightforward. It is a common, widespread species that does not seem to include more than one unit, although one never knows.

SUPRA-SPECIFIC RELATIONSHIPS.— It is MacFarland (1906) himself who re-allocated *nobilis* from *Montereina*, a monotypic genus he had just named, into *Anisodoris* Bergh, 1898. For many years, *nobilis* has remained into *Anisodoris*, except when it was mistakenly placed in *Archidoris* by Michel (1976), until Valdés (2002) re-allocated it to *Peltodoris*. The main reason for this transfer was that the type species of *Anisodoris*, (*Doris punctuolata* d'Orbigny, 1837), by subsequent designation (O'Donoghue 1926:207), is a species with caryophyllidia on its dorsal notum, whereas most other *Anisodoris* species do not have caryophyllidia, including *nobilis*.

A phylogenetic test of the relationships of *nobilis* shows that *nobilis* does not belong to the clade *Peltodoris*, but rather belongs to a large metaphyletic group of species at the base of *Discodorididae* (to which *punctuolata* belongs as well). So, *nobilis* can only be placed in "*Montereina*." The Linnaean binomial of *nobilis* should be "*Montereina*" *nobilis*. Possible names under the *ICPN* are "*Montereina*" *nobilis* or simply *Discodorididae nobilis*.

"*Montereina*" *notha* (Bergh, 1877) New combination
Discodorididae notha (Bergh, 1877) New combination

Figures 309-310.

Discodoris notha Bergh, 1877a:530-532, plate LXI, figs 29-30, plate LXII, figs 3-9.— Bergh, 1904:53-54, plate IV, figs 7-14.

Type material.— Lectotype (ZMUC GAS-2127), designated here, one specimen 27/17 mm (#1) preserved, leg. Riise, 1860. Three paralectotypes are designated here: one specimen (ZMUC GAS-2127) 20/14 mm (#2) preserved, leg. Riise, 1860; two specimens (ZMUC GAS-2126) 45/27 (#1) and 36/20 (#2) mm preserved, leg. Schramm, [no collecting date], [first called *D. crucis* by Mørch]. Prior to the present study, the type material of *notha* included four syntypes. A lectotype is designated here to solve a nomenclatural issue. Indeed, two specimens (ZMUC GAS-2126), which do not fit with the original description, are part of a different species, *Discodorididae branneri*. The original description of *notha* does not mention the penis fully covered with spines, diagnostic of *branneri*, and found in specimens #1 and #2 of ZMUC GAS-2126. Bergh overlooked this penis in these two specimens. One cannot exclude that he also overlooked it in the two other specimens (ZMUC GAS-2127). However, it is more likely that these two other specimens actually were part of a different entity (see below). If one of the two specimens that are part of *branneri* had been selected as a lectotype, *branneri* would have become a junior synonym of *notha*. However, this solution is rejected here because the original description of *notha* does not mention the diagnostic character of *branneri*, i.e., a penis measuring up to 11 mm long, covered with spines. Because the original description is largely based on the two other syntypes (ZMUC GAS-2127), one of these two specimens was selected as the lectotype so that its anatomy matches the original description. Consequently, the fact that two types (ZMUC GAS-2126 #1 and #2) are part of *branneri* is no longer an issue because only the lectotype has a name-bearing function; addressing the identity of *notha* and the nomenclatural status of the name *notha* is no longer jeopardized by the fact that two type specimens are part of a different species. In order to avoid any confusion, the two specimens of the lot ZMUC GAS-2127 are distinguished as specimens # 1 and #2. The lectotype is the specimen #1. Also, the two paralectotypes from Guadeloupe (ZMUC GAS-2126) are referred to as specimens #1 and #2.

Type locality.— The type locality of *notha* is the locality of the lectotype selected here: St. Thomas, [Virgin Islands]. Note that a paralectotype (ZMUC GAS-2127 #2) is also from the type locality, and that two other paralectotypes (ZMUC GAS-2126) are from Guadeloupe.

Type material condition.— The lectotype (ZMUC GAS-2127 #1) and two paralectotypes (ZMUC GAS-2127 #2, ZMUC GAS-2126 #1) were dissected by Bergh. Several pieces of organs remain, in addition to the three body walls: three digestive glands, two intestines (ZMUC GAS 2126 #1, ZMUC GAS-2127), a penis (ZMUC GAS-2126 #1), and an ampulla (ZMUC GAS-2126 #1). The third paralectotype (ZMUC GAS-2126 #2) was dissected for the present study.

Remarks on the original description (Figs. 309-310).— Fortunately, surprisingly, and interestingly, Bergh carefully distinguished the characters he found in the "small" specimens from St. Thomas (ZMUC GAS-2127) from the characters he found in the "large" specimens from Guadeloupe (ZMUC GAS-2126). However, the original description is largely based on the small specimens. Bergh only added a few comments on the large specimens. Preserved, these four specimens are externally very similar: according to Bergh, they were yellowish-grayish with darker spots on the dorsal notum; 125 years later, they are colorless, whitish, with or without traces of faded irregular darker spots on the dorsal notum and ventral brown dots on the ventral surface. All specimens have six tripinnate branchial plumes, two digitiform, ungrooved, oral tentacles, a bilabiate anterior foot with a notched superior lip, simply hamate teeth, etc. However, these characters are shared by all discodoridids and do not help us identify *notha*. Bergh described a high, muscular cone, near the penial aperture. This structure, illustrated by Bergh (1877a, plate LXI, fig. 30), could be the muscular wall found in *Tayuva*, although one can hardly be positive about this. Bergh mentioned this accessory muscular cone in the reproductive system of the small specimens. However, he did not specify whether or not he saw it in the large specimen he dissected. However, it is likely that he did not see a muscular cone in the large specimen. Indeed, a penis diagnostic of *Discodorididae branneri* at the bottom of the jar with the specimens from Guadeloupe, and *branneri* does not have a muscular wall in the distal part of the reproductive system. Also, the other specimen (ZMUC GAS-2126 #2), left entire by Bergh and dissected for the present study, had the same penis. Bergh only described an unarmed papilla in the original description of *notha*: he only considered the two specimens from St. Thomas (ZMUC GAS-2127) for the penial morphology, and did not take into account the third specimen he had dissected from Guadeloupe (ZMUC GAS-2126 #1). The original description of *notha* should exclude the different passages where Bergh referred to the "large" specimens from Guadeloupe. This is why one of the two "small" specimens from St. Thomas was selected as the lectotype.

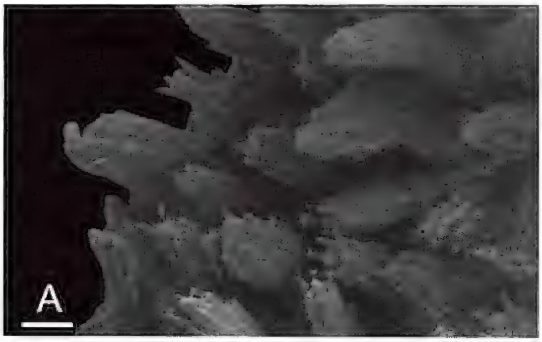

FIGURE 309. *Discodorididae notha*, dorsal notum, tubercles, lectotype, ZMUC 2127. A. Scale = 100 μm.

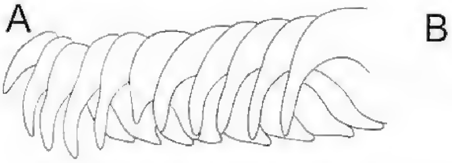

FIGURE 310. *Discodorididae notha*. A. Lateral teeth, after Bergh (1877a: plate LXII, fig. 7).— B. Muscular cone, after Bergh (1877a: plate LXI, fig. 30).

DISCUSSION.— Although it is clear that two paralectotypes (ZMUC GAS-2126 #1 and #2) are part of *Discodorididae branneri*, the identity of *notha* and the nomenclatural status of *notha* remain uncertain. One of the few characters that could help us identify *notha* is the "muscular cone" described by Bergh in the two specimens (lectotype and paralectotype) from St. Thomas (ZMUC GAS-2127). However, this "muscular cone" described by Bergh could not be found (the reproductive systems dissected by Bergh are not in the jar and probably lost). This structure could be the distal muscular wall of *Tayuva*, but this is uncertain.

Here, *notha* is regarded as a *nomen dubium*. The two paralectotypes from Guadeloupe, which provide useful information about the anatomy of *Discodorididae branneri*, are described with other specimens of *branneri*. The two specimens from Guadeloupe had originally been identified as *Doris crucis* by Mörch, and that the type material of *crucis* also includes a specimen that is actually part of *branneri* (see *crucis*). Bergh (1877a) described another species, *muta*, which might also be a synonym of *Tayuva lilacina*. Finally, Bergh (1904) identified a specimen as *notha* from Puerto Rico. However, he did not mention any characters that could allow us to determine whether this specimen, which could not be found, is part of *branneri* or something else, such as *notha*.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *notha* shows that *notha* does not belong to the clade *Discodoris*, but rather is part of a large metaphyletic group of species at the base of *Discodorididae*. So,the Linnaean binomial of *notha* should be "*Montereina*" *notha*. Possible names under the *ICPN* are "*Montereina*" *notha* or simply *Discodorididae notha*.

"*Montereina*" *opisthidia* (Bergh, 1877) New combination
Discodorididae opisthidia (Bergh, 1877) New combination

Figure 311.

Discodoris opisthidia Bergh, 1877a:528-530, plate LXI, figs 16-18, plate LXII, figs 10-14.

Type material.— Holotype (ZMUC GAS-2125), by monotypy: one specimen 15/8 mm preserved, leg. Semper, November 1859.

Type locality.— Masoloc, Zamboanga, Philippines.

Type material condition.— The holotype, dissected by Bergh, probably dried for a while. It is shapeless and brown. No internal organs remain in the jar. No slides could be found.

Distribution.— The holotype is the only specimen known.

Remarks on the original description (Fig. 311).— The holotype is covered with tubercles that do not seem to be caryophyllidia. The original description is general and does not provide any diagnostic feature that could help us re-identify *opisthidia*. The color of the dorsal notum (greenish-yellow), based originally on a preserved specimen, is not helpful. Radular features are not informative either: teeth simply hamate, formula of 30 × (52-0-52). More importantly, Bergh could not describe the reproductive system because the holotype was immature.

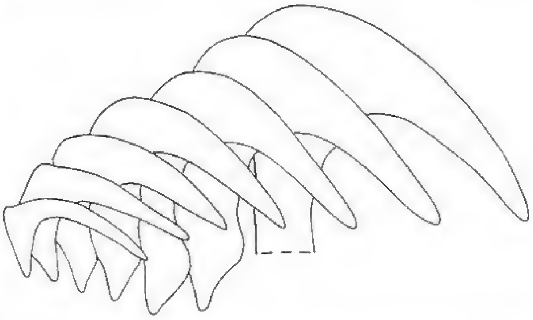

Figure 311. *Discodorididae opisthidia*, outermost teeth, after Bergh (1877a: plate LXI, fig. 12).

Discussion.— Here, *opisthidia* is regarded as a *nomen dubium*, because the holotype is in poor condition and because the original description is not informative.

Supra-specific relationships.— A phylogenetic test of the relationships of *opisthidia* shows that *opisthidia* does not belong to the clade *Discodoris*, but simply is part of the metaphyletic group at the base of *Discodorididae* (largely due to lack of sufficient data). The Linnaean binomial should be "*Montereina*" *opisthidia*. Possible names under the *ICPN* are "*Montereina*" *opisthidia* and *Discodorididae opisthidia*.

"*Montereina*" *pallida* (Baba, 1937) New combination
Discodorididae pallida (Baba, 1937) New combination

Figure 312.

Discodoris pallida Baba, 1937b:305-307, fig. 8, plate 1, fig. 11.

Type material.— One holotype, by monotypy: one specimen 15 mm alive, [leg. probably Baba], October 1935. The holotype was probably deposited at the Amakusa Marine Biological Laboratory. However, it is lost, like most of the types that Baba designated before World War II (personal communication, Dr. Yoshi Hirano).

Type locality.— Tomioka, Amakusa [32/33° S, 129/130° E], Japan.

Distribution.— The holotype is the only specimen known.

Remarks on the original description (Fig. 312).— The original description is incomplete. In particular, the reproductive system was not described. Most characters mentioned are shared by most or many discodoridid species, such as the presence of digitiform oral tentacles, an anterior, bilabiate foot with a deeply notched upper lip, and a labial cuticle armed with jaws. However, a few characters

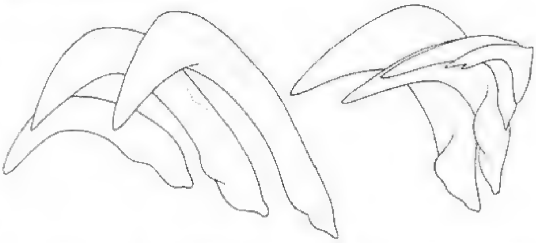

Figure 312. *Discodorididae pallida*, innermost and outermost teeth, after Baba (1937b: fig. 8A).

are less common, such as, the pointed tail of the foot, and the presence of nine gills. Baba described the body as covered with "villous papillae," but the term 'villous' is unclear and it is unclear whether or not the dorsal notum of *pallida* was covered with caryophyllidia. Finally, the color is quite diagnostic: ashy yellow ground color, darker towards the median line, bearing a small number of dark brown 'flecks,' the majority of them in the mid-dorsal region and the tip of the papillae being dark brown (see Baba, 1937b: plate 1, fig. 11).

Discussion.— The name *pallida* remains a mystery. At fisrt, it seemed that it could refer to a *Paradoris* specimen, but the radular formula −15 × (14/17-0-14/17)− is incompatible with the elongated radulae found in *Paradoris*. Also, no *Paradoris* specimen is known with 'split outermost teeth.' Moreover, this would imply that Baba forgot to mention that the grooved oral tentacles, and the third ventral jaw on the labial cuticle. Therefore, the name-bearer of *pallida* does not belong to *Paradoris*. The shape of the outermost teeth (not spatulate) indicates that it does not belong to *Geitodoris* either. As Baba mentioned, *pallida* "closely resembles the Californian form *Discodoris heathi* MacFarland in colours, but differs from it in the type of the radula." All the specimens examined from Japan were collected in Okinawa (mainly by Robert Bolland), in the tropical waters of the Ryukyu Islands. The holotype of *pallida* was collected at the northern limit of the tropical waters, an area from which no specimen was available. The name *pallida* must be kept as an available name until new specimens can be collected from the type locality.

Supra-specific relationships.— A phylogenetic test of the relationships of *pallida* shows that *pallida* does not belong to the clade *Discodoris*, but simply is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial should be "*Montereina*" *pallida*. Possible names under the *ICPN* are "*Montereina*" *pallida* and *Discodorididae pallida*.

"*Montereina*" *pardalis* (Alder and Hancock, 1864) New combination
Discodorididae pardalis (Alder and Hancock, 1864) New combination

Figures 313-314.

Doris pardalis Alder and Hancock, 1864:117, plate XXVIII, fig. 3.
Discodoris pardalis.— Bergh, 1877a:519; 1878: XXXII.— Bergh, 1884a:93.— Eliot, 1906c:1004-1005.— Eliot, 1906b:651.— Baba, 1933:276-277, fig. 3.— Baba, 1937b:305, plate I, fig. 3.— Baba, 1955:19, 47, plate IX, fig. 24.
Discodoris pardalis var.— Eliot, 1906a:554.

Type material.— Holotype, by monotypy (NEWHM, No. 30): one specimen 35/26 mm preserved, leg. Sir Walter Elliot, [likely 1853-1854]. The NEWHM also holds a slide with the armed, labial cuticle, and the radula (an old label reads "*D.pardalis* / Mr Elliot / No. 30" and the new label reads "3/23/15").

Type locality.— Madras, [Indian Ocean].

Type material condition.— The type was fully dissected (probably by Alder and Hancock) and no internal organs remain in the jar, except for some pieces of the digestive gland. The six branchial plumes are still present as well. The oral area is destroyed. Even the preserved color cannot be determined because the median area of the dorsal notum is poorly preserved (it is basically destroyed). However, the edges are creamish bearing irregular dark spots. The ventral surface is creamish with some slightly darker areas. Eliot (1906c) re-examined the type material of *pardalis* and made a few interesting comments, especially on the radula.

Distribution.— The holotype seems to be the only specimen known. Eliot (1906c) recognized that the specimen he had identified (Eliot 1906a) as *pardalis* from the Maldives was actually not part of *pardalis*. Also, the specimens that Baba (1955) described as *pardalis* from Japan might not be part of this species (see discussion). Note that Baba (1937b) just mentioned the presence of *pardalis* in Japanese waters, with no real description (except for a drawing of the dorsal color). Bergh (1884a) mentioned the name *pardalis* in a list of *Discodoris* species without adding new data.

Remarks on the original description (Fig. 313).— Alder and Hancock described the dorsal color as "yellowish, pretty regularly covered with rufous spots, inclining to orange, largest towards the center of the back" and the ventral color as "pale yellowish white, with faint reddish spots." When he re-examined the type, Eliot (1906b:651) mentioned that it corresponded "with Alder and Hancock's description of the external characters." A century later, the type is largely destroyed and does no longer correspond to Alder and Hancock's description. The foot is rounded anteriorly and posteriorly. The anterior foot is bilabiate, and, according to Alder and Hancock, not notched. They overlooked the notch in *fragilis* as well. Alder and Hancock also described the branchial aperture as "lobed." However, it is not lobed as in *Platydoris* species. Alder and Hancock briefly described the radula: "as in *D. tuberculata*." Eliot (1906b) described the radula (but did not draw it): he found a formula of 28 × (30-0-30), which is correct. The teeth are simply hamate, with no denticles. No diagnostic or peculiar features could be found in the radular teeth. Note that the labial cuticle is armed with jaw plates.

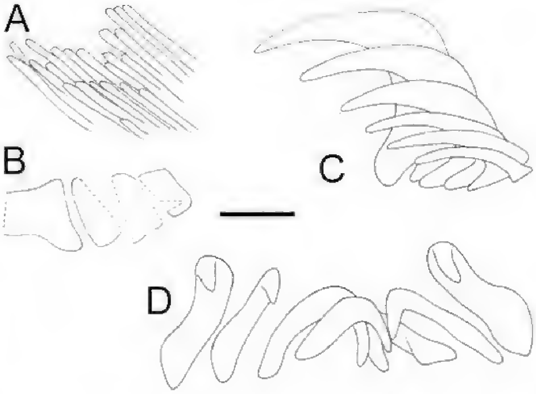

Figure 313. *Discodorididae pardalis*, holotype, slide NEWHM 3/23/15, as currently preserved. A. Jaw rodlets, scale = 40 μm.— B. Jaws, scale = 0.6 mm.— C. Outermost teeth, scale = 50 μm.— D. Innermost teeth, scale = 50 μm.

Discussion.— In the original description, Alder and Hancock admit that *Doris pardalis* "bears great resemblance" to *Doris concinna*, which they describe in the same article. The two differences that they mention between *pardalis* and *concinna* are weak, especially given the small number of specimens considered by Alder and Hancock: dorsal tubercles smaller (in *pardalis*), and the blotches on the dorsal notum "more regular and of a different color." It cannot be excluded that *pardalis* could be part of *concinna*, and thus be small specimens of *Sebadoris fragilis* (see *Discodorididae concinna* and *Sebadoris fragilis* for discussion). However, this is just a hypothesis.

It is nearly impossible to re-identify *pardalis* for several reasons: 1) no distinct features were indicated in the original description; 2) the type material is largely destroyed and uninformative; 3) it was compared by the Alder and Hancock to another species whose identification has always been problematic (*concinna*); 4) the features that can be observed now on the radula or the body wall are general discodorid features. Therefore, *pardalis* is regarded as a *nomen dubium*.

Previous authors also have struggled with the identification of *pardalis*. Eliot (1906a) "doubtfully" identified a specimen of *Discodoris pardalis* (as a different variety), and wrote again latter (Eliot 1906c), after having examined the type, that it was "doubtful" that the specimen identified as *pardalis* could be referred to this species. It is, by the way, difficult to know what Eliot (1906a) identified as *pardalis*: the narrow radula (13/14-0-13/14) he mentioned for a 44 mm long specimen, preserved, suggests that it could have been a *Paradoris*, but Eliot did not indicate the number of rows.

Baba (1933, 1937b, 1955) described *pardalis* specimens from Japanese waters in three publications. Baba's color drawings (Baba 1937b: plate 1, fig. 3; Baba 1955: plate IX, fig. 24) are similar, and Baba probably used the name *pardalis* for specimens that are part of the same entity. His first description (Baba 1933) of *pardalis*, based on a specimen from Amakusa, is vague, and just accompanied by a black-and-white drawing that is not helpful. Baba (1937b) mentioned *pardalis* in Japanese waters, with no description except for a color illustration (Fig. 314). Later, Baba (1955) mentioned additional specimens of *pardalis* from Sagami Bay (many specimens collected in 1946 and 1951). Baba did not justify his identification, which was probably based on a yellowish dorsal background and some brown blotches. However, Baba (1955) described the back as "thickly granulated, in places the largest granules showing tendency of being arranged in reticulate [whitish] figures." This suggests that his specimens may belong to *Sclerodoris*, but this is hypothetical. However, those reticulate figures of large granules are absent in the type material and Baba's *pardalis* specimens and the type of *pardalis* may not be part of the same species. Finally, the black-and-white drawing for a specimen of *pardalis* from Toyama Bay, by Abe (1964:53, plate 24, fig. 88) can hardly be used.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *pardalis* shows that *pardalis* does not belong to the clade *Discodoris*, but simply is part of the metaphyletic group at the base of *Discodorididae*, largely because of lack of sufficient data. The Linnaean binomial should be "*Montereina*" *pardalis*. Possible names under the *ICPN* are "*Montereina*" *pardalis* and *Discodorididae pardalis*.

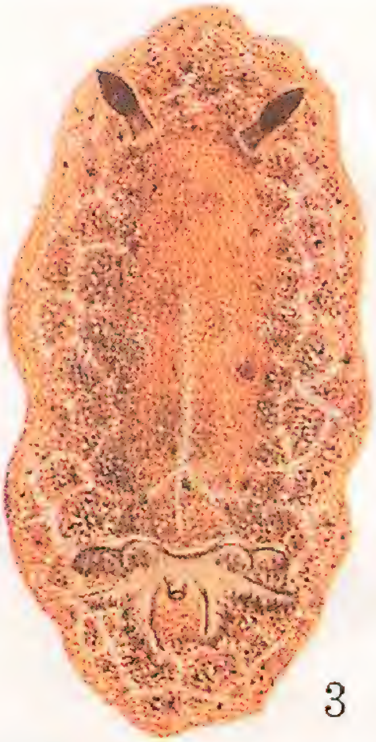

FIGURE 314. *Discodorididae pardalis*, dorsal color of *Discodoris pardalis* by Baba (1937b: fig. 3). Baba's identification is doubtful.

"*Montereina*" *paroa* (Burn, 1969) New combination
***Discodorididae paroa* (Burn, 1969) New combination**
Figures 315-316.

Discodoris paroa Burn, 1969:86-88, figs 30-34.

TYPE MATERIAL.— Holotype (NMV F27123), by original designation: one specimen 16/7 mm, leg. Tom Crawford, 27 May 1962.

TYPE LOCALITY.— Shoreham, Westernport, Victoria, Australia.

TYPE MATERIAL CONDITION.— The holotype was dissected by Burn. The oral area and the anterior foot are destroyed. The radula, dissected by Burn, was mounted on a SEM stub for the present study. The labial cuticle is missing. The reproductive system is missing as well.

ADDITIONAL MATERIAL DISSECTED.— **Australia**, Victoria, Corner Inlet, Nooramunga, one specimen 8/5 mm in preserved length, leg. D. A. Staples, 21 February 2001, 1.5 m depth (scuba), determined as *Discodoris paroa* by Robert Burn (NMV F96224) [however, this specimen is *not* part of the same entity as the holotype of *paroa*].

REMARKS ON THE ORIGINAL DESCRIPTION (Figs. 315-316).— The live animal was "bright red with dark brown spots, the branchiae were red and the rhinophores dark brown." The dorsal notum of the preserved holotype is currently colorless, as described by Burn: "dull cream with dark brownish mottling all over the notum." The ventral surface is also creamish. Burn described "low papillae" on the dorsal notum. The notum is currently almost entirely embedded in a thick matrix, and no distinct tubercles can be observed. The tubercles, which Burn described as papillae with "from one to four" protruding spicules, may not be caryophyllidia (Burn 1969: fig. 31). However, the presence of caryophyllidia cannot be totally excluded. The oral tentacles are conical and, as mentioned by Burn, somewhat flattened, which may be an artifact. The anterior foot, which was destroyed and thus can no longer be observed, was described as bilabiate and notched by Burn. Ten rhinophoral lamellae were counted (Burn mentioned at least eight lamellae). The labial cuticle is armed with two jaw plates. The radula, left in a separate jar by Burn, was re-examined. The radular formula seems to 50 × (75-0-75) although Burn counted fewer teeth per half row (70 teeth), which is not a significant difference. However, Burn overlooked some tiny detail that he could not see under a dissecting scope. The teeth are not smooth: all teeth, except for the last five (or so) outermost teeth bear an outer denticle. Also, the last outermost tooth is pectinate (with three to five short rounded denticles). Burn did not describe the reproductive system, which he unfortunately removed.

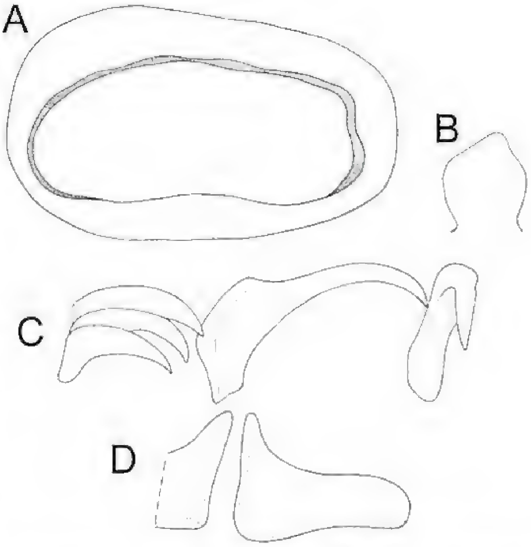

FIGURE 315. *Discodorididae paroa*, radula, holotype, MV F27123. A. Ventral side, as currently preserved, total length = 16 mm.— B. Oral tentacle, total width = 0.6 mm.— C. Radular teeth, after Burn (1969: fig. 34).— D. Jaws, after Burn (1969: fig. 33).

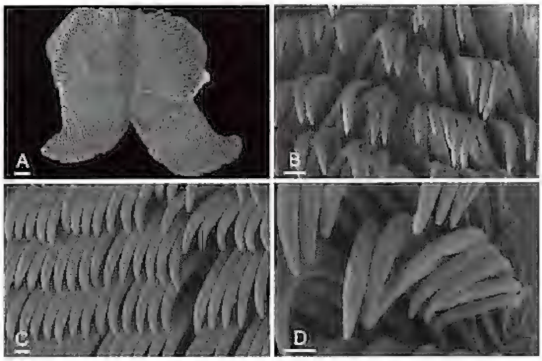

FIGURE 316. *Discodorididae paroa*, radula, holotype, MV F27123. A. Scale = 300 μm.— B. Innermost teeth, scale = 20 μm.— C. Median teeth, scale = 20 μm.— D. Outermost teeth, scale = 20 μm.

DISCUSSION.— The identification of *paroa* does not seem to be easy: in fact, its author, Robert Burn, identified in 2001 a specimen as *paroa* which is actually not part of *paroa*. This specimen, alive, was (as indicated on the label): "deep red, as the bryozoan *Mucropetroliella* (?) living at the base of *Posidonia*, on which the animal was found." Preserved, the specimen is homogeneously white, including gills and rhinophores. Some of its differences with the holotype of *paroa* are mentioned here. This specimen is a discodorid, and its –poorly preserved– dorsal notum seems to bear caryophyllidia. The labial cuticle is smooth. The radular teeth are simply hamate, smooth, with finely pectinate, *Thordisa*-like, outermost teeth. Some organs of the small and homogeneously white reproductive system could not all be identified (especially the receptaculum seminis). No penial organ seems to be present.

Also, Coleman (2001) published a color picture of a 25 mm long, red sea slug from Mornington, Victoria, which he identified as *Discodoris paroa*. It is not possible to determine whether this identification was correct or not without a dissection. The case of *paroa* is interesting: given that its own author was not able to re-identify it, how can we expect that other people could re-identify it? The fact that the original description of *paroa* is incomplete and based on a single specimen certainly does not help us. If one wishes to know what *paroa* is, one will have to go back collecting from the type locality and look for specimens with a radula and a dorsal color similar to that of the holotype, and then, try to find additional specimens nearby.

Supra-specific relationships.— Burn did not justify his decision of classifying *paroa* within *Discodoris*. However, Burn classified other species (e.g., *Discodoris crawfordi*, *Discodoris turia*) in *Discodoris* just because they would share some plesiomorphic features with discodorids. A phylogenetic test of the relationships of *paroa* shows that *paroa* does not belong to the clade *Discodoris*, but simply is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial should be "*Montereina*" *paroa*. Possible names under the *ICPN* are "*Montereina*" *paroa* and *Discodorididae paroa*.

Some species of *Rostanga* were recently described with radular teeth similar to the teeth of *paroa*: median teeth with an outer denticle, and last outermost teeth with a few apical denticles. Addressing whether or not *paroa* belongs to *Rostanga* would first require addressing whether or not its dorsal notum bears caryophyllidia, which is unfortunately unclear in the holotype. However, same-looking radular tooth denticles are commonly found in discodorids, and *paroa* may not belong to *Rostanga*.

"*Montereina*" *phoca* (Marcus and Marcus, 1967) New combination
Discodorididae phoca (Marcus and Marcus, 1967) New combination

Figures 317-318.

Discodoris phoca Marcus and Marcus, 1967a:78-80, figs 99-101.

Type material.— Holotype (NMNH 576272, slides F818, F819, F820), by original designation: one specimen 50/30 mm preserved, leg. G. Hendrix, [16 June 1963].

Type locality.— Western side of Key Biscayne, Florida.

Type material condition.— Ernst and Eveline Marcus dissected the holotype. The body wall, the digestive gland, and the intestine remain in the jar. However, pieces of the reproductive system, the jaws, and the radula are preserved on three slides. The slide with the jaws and the radula is dry and is in poor condition: the two jaws are largely destroyed.

Distribution.— The holotype is the only specimen known.

Habitat.— The holotype was found feeding on sponges in mangroves.

Remarks on the original description (Figs. 317-318).— Eveline and Ernst Marcus described the dorsal color pattern of the live animal as "purplish brown with a net of white dots, mainly to the sides of the center" based on a photograph that could not be found. The ground dorsal color of the preserved animal is grayish and bears large, light brown blotches, especially in the median part of the notum. The hyponotum of the preserved animal is also grayish and bears many small, light brown dots. Preserved, the gills and the rhinophores are still black. The general appearance of the notum is smooth, although it clearly bears low tubercles. According to Evelyne and Ernst Marcus, those tubercles are caryophyllidia. This could not be confirmed with a dissecting microscope. A small piece of the notum observed in SEM did not help: because of the poor preservation of the notum, it cannot be established whether or not tubercles are caryophyllidia. The digitiform oral tentacles are not grooved. The rest of the description is general: simply hamate teeth (the formula seems to be 25 × (40-0-40) instead of 27 × (42-0-42), but the exact number of rows and teeth is difficult to establish), two prostatic parts in the reproductive system, etc. Note that the Marcus describe an intestine "winding on the right side of the intestinal gland." The presence of intestinal loops was confirmed but their position could not be determined because the intestine was separated from the digestive gland. Eveline and Ernst Marcus drew a "fertilization chamber" in the reproductive system, which they probably did not see by dissection as it is extremely difficult to see. On a slide, a structure was found that could be interpreted as a large unarmed penis or the ampulla (the original description simply mentions the presence of a small penial papilla).

Discussion.— The original description is general and mentions characters that are common among discodoridids. Several important features are unknown, such as the actual organization of the reproductive system (the Marcus' drawing is too schematic). The dorsal color, however, deserves attention. The presence of intestinal loops on the right side of the digestive gland suggests affinities with other species such as *Sebadoris fragilis* and *Sebadoris nubilosa*. Clearly, this species needs to be redescribed with new material from the type locality. The black-and-white drawing of the dorsal notum of *phoca* (Marcus and Marcus 1967a: fig. 99) makes *phoca* look like *Discodorididae branneri*. However, it clearly is a different entity because of the absence of a strongly armed penis in *phoca*.

Supra-specific relationships.— A phylogenetic test of the relationships of *phoca* shows that *phoca* does not belong to the clade *Discodoris*, but simply is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial should be "*Montereina*" *phoca*. Possible names under the *ICPN* are "*Montereina*" *phoca* and *Discodorididae phoca*.

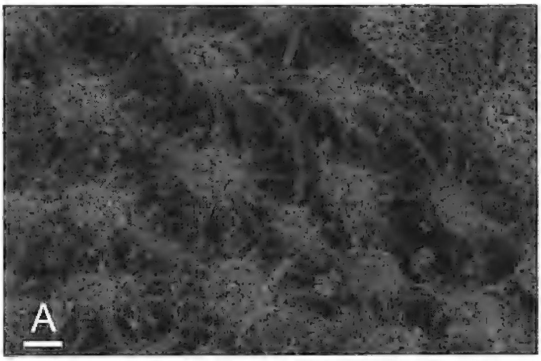

Figure 317. *Discodorididae phoca*, dorsal notum, holotype. A. Tubercles, scale = 100µm.

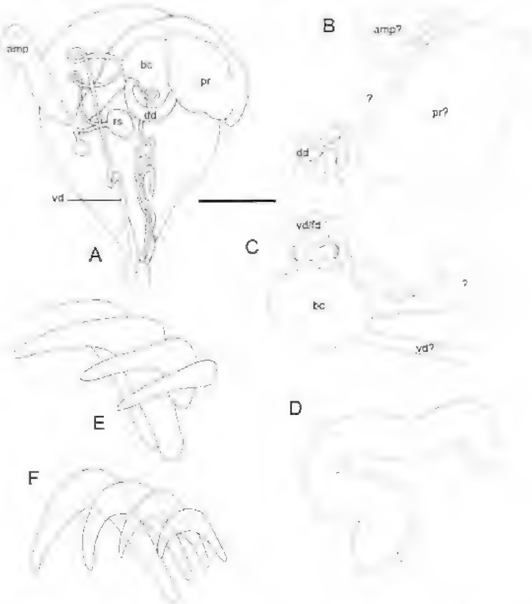

Figure 318. *Discodorididae phoca*, holotype. A. Reproductive system, after Marcus and Marcus (1967a: fig. 101).— B. Reproductive system, as currently preserved (slide F818), identification of organs tentative, scale = 1 mm.— C. Reproductive system, as currently preserved (slide F818), identification of organs tentative, scale = 1 mm.— D. Uncertain identification: copulatory organ, ampulla, or something else (slide F819), scale = 2 mm.— E. Outermost teeth, as currently preserved (slide F820), scale = 50 µm.— F. Outermost teeth, as currently preserved (slide F820), scale = 100 µm.

"*Montereina*" *punctifera* (Abraham, 1877) New combination
Discodorididae punctifera (Abraham, 1877) New combination

Figure 319.

Doris punctata d'Orbigny, 1839:38-39, plate IV, figs 1-5 (name permanently invalid, preoccupied by *Doris punctata* Rüppell and Leuckart, 1831, and *Doris punctata* Quoy and Gaimard, 1832, replaced by *Doris orbignyi* H. & A. Adams, 1858).

Platydoris punctata.— Bergh, 1877b:74.— Bergh, 1878a: XXXIII.

Doris orbignyi H. and A. Adams, 1858:51 (new replacement name for *Doris punctata* d'Orbigny, 1839; name permanently invalid, preoccupied by *Doris orbignyi* Férussac, 1822 [*emend. pro orbigni*], replaced by *Doris punctifera* Abraham, 1877).

Doris punctifera Abraham, 1877:202 (new replacement name for *Doris orbignyi* H. and A. Adams, 1858).

Peltodoris punctifera.— Ortea and Bacallado, 1981:767, 771-774, figs 3, 4, plate I, figs C, E.— Ballesteros et al., 1985:243-244, fig. 10A.

Discodoris punctifera.— Wirtz, 1999:13, plate 3, fig. 8.

TYPE MATERIAL.— The type material could not be found. It is not at the MNHN. The number of specimens observed by d'Orbigny is unclear (probably just one).

TYPE LOCALITY.— Not far from the town of Santa-Cruz, Tenerife, Canary Islands (in August).

DISTRIBUTION.— Canary Islands (d'Orbigny 1839; Ortea and Bacallado 1981; Ballesteros et al. 1985) and Madeira (Wirtz 1999).

HABITAT.— Under rocks in the tidal zone (d'Orbigny 1839; Ortea and Bacallado 1981); at 12 meters depth (Wirtz 1999).

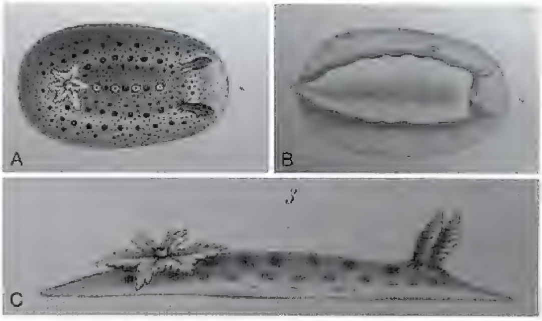

FIGURE 319. *Discodorididae punctifera*, dorsal color of *Doris punctuolata*, original description by d'Orbigny (1839: plate IV, figs 1-3). A. Dorsal view.— B. Ventral view.— C. Lateral view.

REMARKS ON THE ORIGINAL DESCRIPTION (Fig. 319).— The original description is the description published by d'Orbigny, although *Doris punctata* was replaced by a new name. This description contains only some information about the external morphology as well as some information about the color. The live animal(s) measured from 16 to 18 mm. The body is oval, quite flattened, with a wide mantle. The dorsal surface is covered with small, round, tubercles. The morphology of the anterior foot is not described. The oral tentacles are "conical, not too elongated." The internal anatomy is not described. There are six branchial plumes (the branchial sheath is *not* described having six lobes). It looks like d'Orbigny could observe the color of a live animal because he mentions that "[the species] became totally white" when he put it in alcohol. The dorsal color of the live animal was pinkish (background). On the median line, there were three brown-violet blotches, separated by four white blotches with a darker center. There were several other lines of irregular blotches between the median line and the mantle margin: two (one on each side) consist of larger and darker blotches than the other ones.

DISCUSSION.— The original description by d'Orbigny is problematic for several reasons. No anatomical characters are provided. The type is lost. The small live animal might just have been a juvenile. The drawings of the external morphology are not in color. Bergh (1877b:74; 1878a: XXXIII) transferred *Doris punctata* into *Platydoris*, probably because of its flattened body. Despite a flattened body, *punctata* probably is not a *Platydoris*, because d'Orbigny would have probably described the six-lobed branchial sheath, and, also, his drawing of the ventral surface does not show a narrow foot, as in *Platydoris*.

According to d'Orbigny, this species was close to *Doris maculosa* Cuvier, 1804. The latter is quite problematic, and is regard ed here as a *nomen dubium* in this monograph, although Quoy and Gaimard (1932) identified as *Doris maculosa* a specimen that is clearly part of *Sebadoris fragilis* (see this species). Based on the color described by d'Orbigny, his *Doris punctata* could be *Tayuva lilacina* (traditionally referred to as *maculosa* in that region), in which case, the valid name for *Dis-*

codoris punctifera would be the valid name for it. However, this is uncertain, and it would be inappropriate to propose a formal synonymy, especially because the re-description by Ortea and Bacallado (1981) suggests that this hypothesis is incorrect.

Besides the original type material, a few additional, non-type specimens were identified as *Peltodoris punctifera* (Canary Islands) and *Discodoris punctifera* (Madeira). The dorsal color of the specimens of *Peltodoris punctifera* described by Ortea and Bacallado (1981) is globally similar to the color described by d'Orbigny. This similarity in the dorsal color combined with the fact that those specimens were collected near the type locality suggest that Ortea and Bacallado did encounter the same species as the one described originally by d'Orbigny. However, this re-description needs to be commented on. First, it seems that the dorsal notum is covered with caryophyllidia (Ortea and Bacallado 1981: fig. 3D). Second, the maximum size is 25 mm, alive, which is much smaller than the maximum size of *Tayuva lilacina* Bergh (80 mm long), and the 25 mm long specimen seemed mature (based on the size of the female gland mass), all this suggesting that *punctifera* is different from *lilacina*. Third, Ortea and Bacallado dissected only one specimen, which means that the species is still poorly known. For, example, the labial cuticle is supposed to be smooth, but this information needs to be confirmed with additional specimens. Note that the radular teeth are simply hamate and bear no denticles.

The specimen photographed by Wirtz (1999) in Madeira and identified as *Discodoris punctifera* could be part of *punctifera*, although it is unclear given that this identification should probably be addressed with anatomical data (along with additional dissections of specimens from the Canary Islands). Interestingly, the specimen photographed by Wirtz could almost look like a *Platydoris* (with a flattened body).

In summary, *punctifera* is not regarded as a poorly known species, because there is hope that we could re-identify it, especially with more material from the type locality.

Supra-specific relationships.— A phylogenetic test of the relationships of *punctifera* shows that *punctifera* does not belong to the clades *Discodoris* or *Peltodoris*, but simply is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial should be "*Montereina*" *punctifera*. Possible names under the *ICPN* are "*Montereina*" *punctifera* and *Discodorididae punctifera*.

Future studies.— The anatomy of *punctifera* is known from only one specimen: this species needs to be redescribed (specimens from the Canary Islands would be ideal) with multiple specimens, so we can know more about its infra-specific variation. Several anatomical questions still need to be addressed such as, the presence/absence of jaws, and the presence/absence of caryophyllidia. SEM pictures of the radula are needed.

"*Montereina*" *punctuolata* (d'Orbigny, 1837) New combination
Discodorididae punctuolata (d'Orbigny, 1837)

Figures 320-322.

Doris punctuolata d'Orbigny, 1837:187, pl. 16, figs 4-6.
Diaulula punctuolata.— Valdés and Gosliner, 2001:136-138.— Schrödl, 2003:39-41, figs 20, 56, 74.
Discodorididae punctuolata.— Dayrat and Gosliner, 2005:205.
Doris vestita Abraham, 1877:203, 252, plate XXVIII, figs 5-6.
Discodoris vestita ?.— Bergh, 1878a: XXXVIII.— Bergh, 1884a:93.
Diaulula vestita.— Eliot 1907a:355-356.— Odhner, 1926:89-91, figs 73-78.— Schrödl, 1996:27.— Schrödl, 2003:39-41, figs 20, 56, 74.

Type material (*vestita*).— Two syntypes (NHM 1869.6.5.95 and NHM 1869.6.5.93), two specimens 40/35 and 35/20 mm preserved, leg. Dr. Cunningham, Pres. Lords of the Admiralty, 1868. The labels distinguish a holotype (NHM 1869.6.5.95) and a paratype (NHM 1869.6.5.93). However, these designations are invalid because there was no original designation by Abraham and because his description is based on more than one specimen (the exact number was not specified by Abraham). Therefore, these specimens are syntypes. Also, a label indicates that one specimen was sent to Eliot in a separate bottle on June 11, 1907: it is not specified whether or not this specimen was sent back to the Museum. Finally, Dr. M. Schrödl examined both specimens (lot returned in 1999).

Type locality (*vestita*).— Otter Island (NHM 1869.6.5.95) and Sholl Bay (NHM 1869.6.5.93), Straits of Magellan.

Type material condition (*vestita*).— One specimen (NHM 1869.6.5.95) is almost complete: it was opened on the ventral side and the radula was removed, but all the other organs remain; a small piece of the notum was cut (not for the present study). The other specimen (NHM 1869.6.5.93) was entirely dissected prior to the present study: the foot and the notum are apart. The buccal mass was removed and neither the radula nor the labial cuticle could be found; the reproductive system is in pieces, and the receptaculum seminis, the deferent duct, the atrium, the penial sheath, the vagina, and most certainly the prostate are missing.

Other material examined (not dissected).— **Chile**, Lacuay Peninsula, Chiloe Island, 10 meters depth, 24 December 1994, one specimen 60/45 mm preserved, leg. S. Millen, M. Schrödl, and S. Gigglinger, identified as *Diaulula punctuolata* by A. Valdés (CASIZ 118012) [specimen dissected by A. Valdés and T. M. Gosliner, some pieces of the reproductive system remain in the jar; voucher of Valdés and Gosliner (2001); a piece of notum was prepared for SEM].

Distribution.— Magellanic: from northern Argentina over Patagonia and the Falklands, up to Valparaiso, central Chile (see Schrödl 2003, as *Diaulula punctuolata*).

Remarks on the original description (*vestita*, Figs. 320-322).— The color of the live animal was unknown. Abraham described "yellowish or light brown, with an orange or pinkish tinge upon the foot" spirit specimens. Preserved types are currently whitish, homogeneously. The "very convex" back is probably caused by preservation. The narrow, elongated tubercles are caryophyllidia. The number of branchial plumes (Abraham described seven plumes) could not be determined: there are between six to nine plumes. The anterior foot is bilabiate, with a notched upper lip. Abraham mentioned a radula with 13 rows of "elongated recurved" teeth (and with no rachidian tooth). The reproductive system was not described by Abraham. The different pieces that remain in the jar are hardly informative.

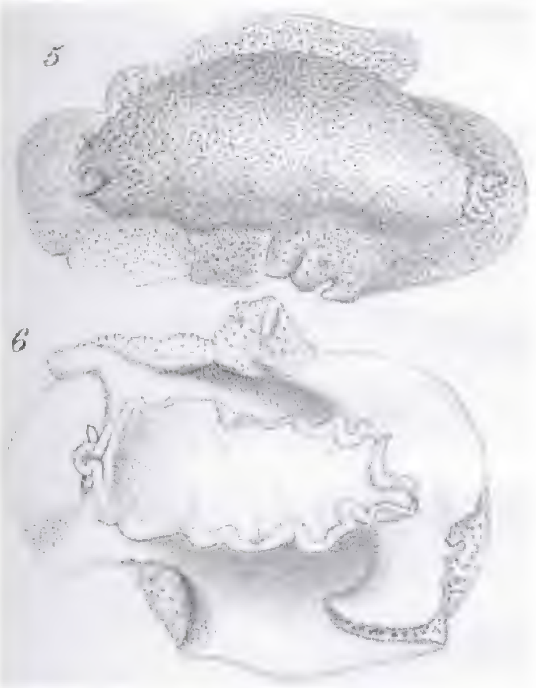

Figure 320. *Discodorididae punctuolata*, dorsal and ventral view of *Doris vestita*, original description by Abraham (1877: plate XXVIII, figs 5-6).

Discussion.— Schrödl (2003) proposed that *vestita* be regarded as a synonym of *Diaulula punctuolata* (d'Orbigny, 1837), after he had pointed out that *vestita* and *punctuolata* were similar

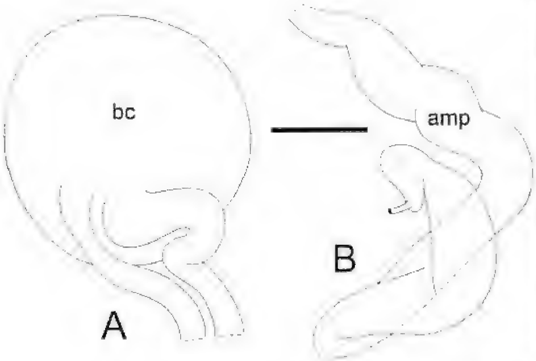

FIGURE 321. *Discodorididae punctuolata*, paratype of *Doris vestita*, remaining pieces of the reproductive system. A. Bursa copulatrix, scale = 1 mm.— B. Ampulla, scale = 2 mm.

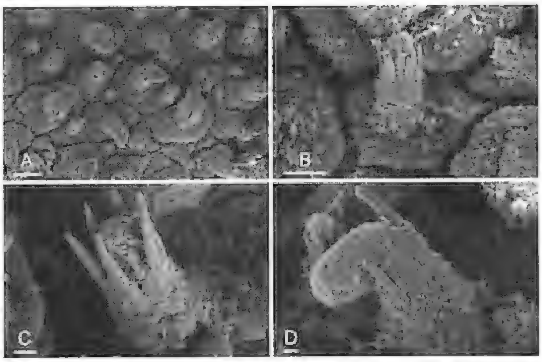

FIGURE 322. *Discodorididae punctuolata*, dorsal notum, CASIZ 118012. A. Dorsal tubercles, scale = 200 µm.— B. Dorsal tubercle, scale = 100 µm.— C. Dorsal tubercle, scale = 30 µm.— D. Dorsal tubercle, scale = 30 µm.

externally, and that Valdés and Muniain (2002) had suggested that "it [was] very likely that both names [were] synonyms." This synonymy seems to be correct. The reader can find more information in Schrödl's (2003) recent synthesis on the taxonomy of *punctuolata*.

SUPRA-SPECIFIC RELATIONSHIPS.— Bergh (1878a) classified *Doris vestita* in *Discodoris*, with two question marks to indicate that the affinities of *vestita* were uncertain. A few years later, Bergh (1884a) simply mentioned the name *vestita* in a list of *Discodoris* species without adding new data, and still with a question mark. Then, Eliot (1907a) transferred *vestita* to *Diaulula*, in which it has remained (Odhner 1926; Schrödl 1996, 2003; Valdés and Muniain 2002).

A phylogenetic test of the relationships of *punctuolata* shows that it does not belong to any of the subclades of *Discodorididae*. It is just part of a large metaphyletic group at the base of *Discodorididae*. Moreover, *Diaulula* is not monophyletic. Therefore, the Linnean name should be "*Montereina*" *punctuolata*. Possible names under the *ICPN* are "*Montereina*" *punctuolata* and *Discodorididae punctuolata*.

"*Montereina*" *purcina* (Marcus and Marcus, 1967) New combination
Discodorididae purcina (Marcus and Marcus, 1967) New combination

Figure 323.

Discodoris purcina Marcus and Marcus, 1967a:81-82, figs 102-104.

TYPE MATERIAL.— Holotype (NMNH 576281, slide F831), by original designation: one specimen 24/16 mm preserved, leg. F. Bayer [and E. Deichmann, according to the original description], [1962].

TYPE LOCALITY.— Biscayne Key, SW Point, Florida.

TYPE MATERIAL CONDITION.— The type was dissected by Eveline and Ernst Marcus. The radula is preserved on a slide (F-831). The reproductive system could not be found. Only the body wall and the digestive gland remain in the jar.

DISTRIBUTION.— The holotype is the only specimen known.

REMARKS ON THE ORIGINAL DESCRIPTION (Fig. 323).— The color of the live animal is unknown. The Marcus described a "transparent greyish" notum with "fine black granules." The preserved specimen is homogeneously whitish, including the rhinophores and gills, which were blackish and blash, respectively, in the original description. The exact nature of the tubercles could not be determined with a dissecting scope. However, they do not seem to be caryophyllidia. The

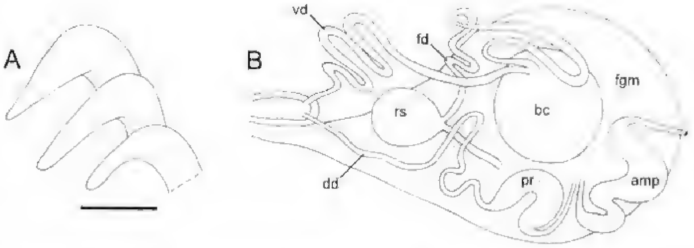

FIGURE 323. *Discodorididae purcina*, holotype, NMNH 576281. A. Outermost teeth, as currently preserved on very dry slide, scale = 50 µm.— B. Reproductive system, after Marcus and Marcus (1967a: fig. 104).

Marcus counted 20 rhinophoral lamellae: this number could not be verified because both rhinophores are missing. The notch of the upper lip of the bilabiate anterior foot could not be observed because the oral area is partly destroyed. The oral tentacles however, are clearly digitiform, and not grooved. The Marcus gave a radular formula of 16 × (43-0-43). These numbers could not be verified because the slide dried and the radula can hardly be observed. The radula is 4 mm wide and 3 mm long. The Marcus thought this radula was "exceptionally short" and regarded it as a diagnostic feature of *purcina*. Its shape does not seem exceptional, and it probably could not help re-identify *purcina*. The reproductive system, unfortunately missing from the type material, is interesting. The exact shape of the prostate, described by the Marcus as "sausage-shape," is unclear: is it flattened (as suggests the fact that there is a clear separation between the prostate and the deferent duct)? Is it tubular? The deferent duct is long and convoluted, as well as the fertilization duct (or called "insemination duct" by the Marcus) and the vaginal duct. The presence and the shape of a penis could not be addressed by the Marcus, which is quite unfortunate because penial structures (when present) are powerful taxonomic features. The bursa copulatrix, spherical, is three times larger than the spherical receptaculum seminis.

DISCUSSION.— The original description of *purcina* is problematic, especially because it lacks some key information: we ignore the color of the live animal as well as whether or not a copulatory organ is present. The long, convoluted genital ducts (the fertilization duct, the deferent duct, and the vaginal duct), however, could help re-identify it. New material from the type locality should help determine whether *purcina* is a valid species name or a junior synonym.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *purcina* shows that *purcina* does not belong to the clades *Discodoris* or *Peltodoris*, but simply is part of the metaphyletic group at the base of *Discodorididae*. The Linnaean binomial should be "*Montereina*" *purcina*. Possible names under the *ICPN* are "*Montereina*" *purcina* and *Discodorididae purcina*.

"*Montereina*" *rubra* (Bergh, 1905) New combination
Discodorididae rubra (Bergh, 1905)

Figures 324-335.

Discodoris rubra Bergh, 1905:104-106, 248, plate I, fig. 7, plate 14, figs 11-14.
Discodorididae rubra.— Dayrat and Gosliner, 2005:205.
Archidoris hawaiiensis Kay and Young, 1969:179-180, figs 4-5.— Kay, 1979:460, fig. 148I. **New synonym.**
Platydoris sp. ["Coleman's *Platydoris*"] Coleman, 2001:61, unnumbered figure.

TYPE MATERIAL (*rubra*).— Lectotype (ZMA 3.05.147), designated here: one specimen 65/45 mm [Bergh measured 75/45] preserved, leg. Siboga expedition, 3 November 1899. Bergh deposited another type specimen at the Zoölogisch Museum, Amsterdam (ZMA 3.05.148). This specimen, also collected during the Siboga Expedition (Gisser Island, Ceram, Indonesia, 28 August 1899, station 172) is part of *Sebadoris fragilis*. It is designated here as a paralectotype. It still is part of the type material of *rubra* but has no name-bearing function. Note that the species name on page 104 (Bergh 1905:104-106) is *Discodoris* ? *sibogae*, not *Discodoris rubra*. However, Bergh (1905:248) published some corrections ("*corrigenda*") at the end of the volume, after the index of names according to which it is perfectly clear that the description that follows the species name *Discodoris* ? *sibogae* is the description of *Discodoris rubra*. Also, concerning the figures, the dorsal notum of *Discodoris rubra* is illustrated on figure 7, not figure 8 (Bergh, 1905: plate I). The figure 8, according to Bergh's "*corrigenda*," represents a species he called *Discodoris sibogae* but for which he did not publish a description. Finally, note that despite the fact that the original description is based on two specimens that do not belong to the same entity, it is not confusing because Bergh smartly distinguished the description of those two specimens.

TYPE MATERIAL (*hawaiiensis*).— According to the original description, a holotype and a paratype were deposited at the B. P. Bishop Museum, Honolulu, Hawaii. However, Kay and Young (1969) mentioned three specimens in total: two specimens collected in Kaneohe Bay, Oahu, in May 1962, and another specimen collected at Koloa, Kauai, in June 1962. According to the BPBM records, the holotype is the largest specimen (110/50 mm) collected from Kaneohe Bay, and the paratype is the smallest specimen (25/20 mm) collected from Koloa Landing, Kauai. However, the label of the specimen received from the BPBM indicated: "Paratype (BPBM 8920), *Archidoris hawaiiensis* Kay and Young, 1969, Oahu: Kaneohe Bay, May 6, 1962." This suggests that, contrary to what was indicated in the original description, Kay and Young deposited more than one paratype, or that something got mixed up. In any case, the specimen dissected for the present study is part of the type material and is labeled as a paratype: one specimen 21/17 mm preserved, [leg. Alison Kay and David K. Young], 6 May 1962.

TYPE LOCALITY (*rubra*).— Off Pasir Pandjang, west coast of Binongka Island, South of Sulawesi, Indonesia [station 220 of the Siboga expedition]. The depth indicated on the label of the lectotype is "278 m." However, the station 220 of the Siboga expedition included dredgings and trawlings at 278, 55, and 10 meters (see, Volume 1 of the *Reports* of the Siboga expedition). The lectotype probably was collected in shallow waters, "at night, about 10 M. with electric light in net".

TYPE LOCALITY (*hawaiiensis*).— Kaneohe Bay, Oahu, Hawaii. Both the holotype and the paratype were collected from the type locality (although see above).

TYPE MATERIAL CONDITION (*rubra*).— The lectotype of *rubra* was entirely dissected by Bergh. Only an empty body wall remains in the jar. However, the dorsal notum is globally well preserved, with the diagnostic features of the dorsal color illustrated by Bergh in the original description.

TYPE MATERIAL CONDITION (*hawaiiensis*).— The condition of the holotype was not checked. The paratype had not been dissected by Alice Kay and David Young and was globally in good condition.

ADDITIONAL MATERIAL DISSECTED.— **Australia**, Queensland, Capricorn Group, Heron Island, 23°26′S, 151°57′E, 10 October 1980, one specimen 110/70 mm, leg. A. Healy, identified as *Discodoris* by W. B. Rudman (AM C124327) [in the same lot, there are two notum pieces that are part of another specimen]; **Papua New Guinea**, North coast, near Madang, East side "Pig Island" (Tab Island), Barracuda Point, 50 feet maximum depth, 13 January 1988, two specimens 60/37 (#1) mm and 30/20 (#2) mm preserved, leg. T. M. Gosliner, identified as *Discodoris rubra* by T. M. Gosliner (CASIZ 071238); Papua New Guinea, North coast, north of Madang, approx. 1 km South of Cape Croiselles, North of the Quarry near Bunn Village, 30 feet maximum depth, 12 February 1988, one specimen 33/18 mm preserved, leg. T.M. Gosliner, identified as *Discodoris rubra* by T. M. Gosliner (CASIZ 065782); **Indonesia**, Manado, off the coast of Sulawesi, 14 May 1992, one specimen 35/22 mm preserved, leg. P. Fiene, identified as *Discodoris rubra* by T. M. Gosliner, (CASIZ 086684); **Thailand**, Gulf of Thailand, off Sattahip, Ko-I-Lao, 3 February 1972, one specimen 58/28 mm preserved, leg. Franz B. Steiner, identified as *Discodoris rubra* by T. M. Gosliner (CASIZ 081904); **Japan**, Ryukyu Islands, Okinawa, Seragaki Beach, 26°30.4′N, 127°52.6′E, 17 July 1992, one specimen 68/32 mm preserved, leg. Robert F. Bolland, identified as *Discodoris rubra* by T. M. Gosliner (CASIZ 087907).

Distribution.— Indo-West-Pacific. Queensland, Australia (present study), Papua New Guinea (Dayrat and Gosliner 2005; present study), Thailand (Dayrat and Gosliner 2005; present study), Indonesia (Bergh 1905, type locality of *rubra*; present study), Japan (Dayrat and Gosliner 2005; present study), Hawaii (Kay and Young 1969, type locality of *hawaiiensis*). The picture published by Coleman (2001) as "Coleman's Platydoris" or "*Platydoris* sp." is the only record of *rubra* from the Indian Ocean (Maldives). Dissections would be needed to confirm the identity of specimens from the Indian Ocean, but we reasonably can expect to find *rubra* in new localities in the Indian Ocean.

WWW.— So far, two pictures of *rubra* have been posted on the *www*. One specimen was found in a reef on the east coast of the Gulf of Thailand (Sattahip District, Chonburi Province), at 7 meters depth, July, 2002 (Bill Rudman's *Sea Slug Forum*, Kitithorn Sanpanich, 26 September 2002, #factsheet of *Peltodoris rubra*). Mike Miller photographed another specimen in Bali, Indonesia (*Mike Miller's Slugsite*, November 2002).

Occurence.— Overall, about 15 specimens are known from the literature (including the present study) and the *www*. This suggests that *rubra* is probably not a common species.

Habitat.— Reef (Bergh 1905), "in shallow water in Kaneohe Bay" and "under a rock in the shallow waters shoreward of the fringing reef near Koloa, Kauai" (Kay and Young 1969), on rocks and coral bottom (CASIZ 081904), on mixed silty sand and coral rubble bottom (CASIZ 087907).

Literature.— Information about the color of the dorsal notum of *rubra* can be found in three contributions (Bergh 1905; Kay and Young 1969, as *hawaiiensis*; Coleman 2001, as *Platydoris* sp.). Bergh (1905) and Kay and Young (1969) also provided some anatomical information, although the descriptions of the reproductive system were incomplete.

Remarks on the original description (*rubra*, Figs. 324A, 325A).— Bergh's illustration of the color of the dorsal notum of *rubra* (Bergh 1905: plate I, fig. 7) helps us identify *rubra*. Note that without this illustration, it would be probably difficult to determine whether or not specimens are part of *rubra*. The darker spots as well as the black dots at the apex of tubercles can still be observed on the dorsal notum of the lectotype. The ventral surface (foot and hyponotum) is creamish and bears some small brown spots and dots. Bergh mentioned the presence of jaws on the labial cuticle, with rodlets 0.075 mm long and 0.005 mm of diameter. However, this was probably erroneous because no jaws were found in any of the specimens dissected for the present study. The radular formula is 44 × (105-0-105), although it is unclear whether 105 is the number of teeth per row or per half row. The description of the anatomy of the reproductive system is brief and incomplete. In particular, the receptaculum seminis and the penial morphology are not described.

Remarks on the original description (*hawaiiensis*, Figs. 325D-H, 326).— Kay and Young (1969) accurately described the color of the dorsal notum as: "red-brown with patches of darker color and minute white spots ocellated with black near the margins." A few of those white ocellated spots can still be observed on the paratype whose color is white and light purple. Kay and Young described five branchial plumae. There are either five or six of branchial plumae in the paratype. The labial cuticle is unarmed. The radular formula found by Kay and Young was 22 × (48-0-48), probably for a 110 mm long specimen. In the 21 mm long paratype dissected here, the radular formula is 16 × (53-0-53). The description of the reproductive system is globally informative (e.g., sausage-shaped receptaculum seminis, called the spermatocyst by Kay and Young; bursa copulatrix, called spermatheca by Kay and Young, three times larger than the receptaculum seminis; deferent duct long and slightly convoluted), but Kay and Young overlooked the peculiar penis within the penial sheath. Finally, Kay and Young mentioned that "a common junction at the albumin and mucous gland is formed by the uterine, prostatic, and ampullary ducts." However, the so-called uterine duct (i.e., the fertilization duct) communicates with the fertilization chamber, not with the ampulla and the prostate.

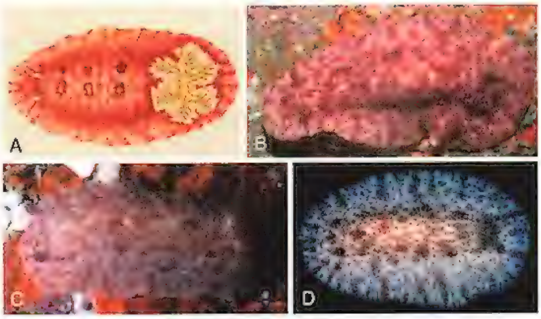

FIGURE 324. *Discodorididae rubra*, dorsal color. A. After Bergh (1905: plate I, fig. 7).— B. CASIZ 071238 (one of two specimens, T.M. Gosliner).— C. CASIZ 065782, total length = 33 mm, preserved.— D. CASIZ 087907, total length = 68 mm, preserved.

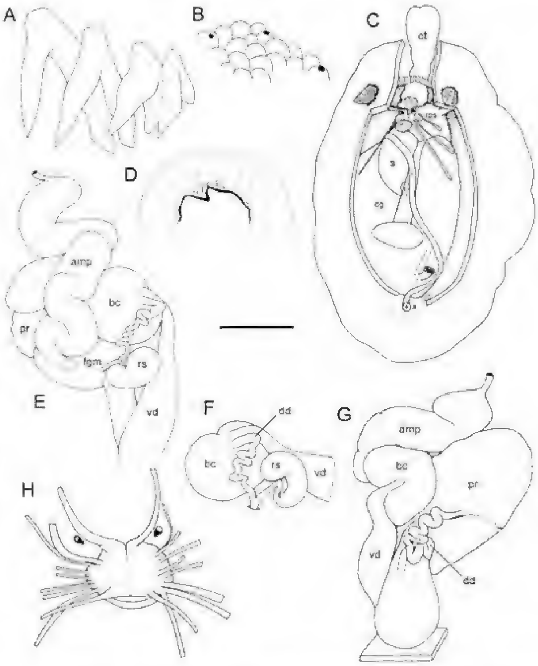

FIGURE 325. *Discodorididae rubra*. A. Outermost teeth, original description of *Discodoris rubra*, after Bergh (1905: plate 14, fig. 14a).— B. Dorsal tubercles, CASIZ 087907, scale = 1.8 mm.— C. Internal anatomy, CASIZ 071238 (#1), total length = 60 mm.— D. Anterior, ventral view, *Archidoris hawaiiensis*, paratype, BPBM 8920, total width = 17 mm.— E. Reproductive system, *Archidoris hawaiiensis*, paratype, scale = 1.2 mm.— F. Spermatic pouches, *Archidoris hawaiiensis*, paratype, scale = 1.2 mm.— G. Reproductive system, *Archidoris hawaiiensis*, paratype, scale = 1.2 mm.— H. Nervous system, *Archidoris hawaiiensis*, paratype, scale = 1.3 mm.

DESCRIPTION OF NEW SPECIMENS (Figs. 324B-D, 325C, 327-335).— *Color*. The dorsal ground color of live animals (CASIZ 065782, CASIZ 071238, CASIZ 071238) is light red-brown or almost white (CASIZ 087907) with darker irregular spots. Some tubercles are bright white, with an apical black spot, which makes them look 'ocellated,' as Kay and Young (1969) would say. The dorsal color of preserved specimens is much lighter, but the darker spots at the apex of some tubercles could be observed in all specimens. After preservation, the foot is creamish, with small brown dots. The ground color of the hyponotum is creamish too, with large irregular dark brown blotches and spots that can form an uninterrupted circular ring around the foot.

External morphology. The body is ovate. The length equals less than twice the width. The largest specimen was 110 mm long. The foot is rounded posteriorly and anteriorly. The width of the foot equals about one third or one half of the width of the dorsal notum (in preserved specimens). The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, but not grooved. The dorsal notum bears tubercles (of different sizes) that are not caryophyllidia. Most of the 'ocellated' tubercles are the largest ones. Many small holes (diameter < 10 µm) and many tufts of cilia were found on the surface of the dorsal notum. In preserved specimens, the margins of the rhinophoral and branchial sheaths can be smooth or crenulate. There are five or six tripinnate branchial plumes arranged in circle around the anus. The rhinophores have from 25 to 45 lamellae.

Digestive system. The stomach is large, freely located on top of the left anterior side of the digestive gland. A small caecum is located on the left posterior side of the stomach. The intestine is straight and dorsal. The labial cuticle is smooth in all specimens. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. Radular formulae were: 21 × (55-0-55) in a 60 mm long

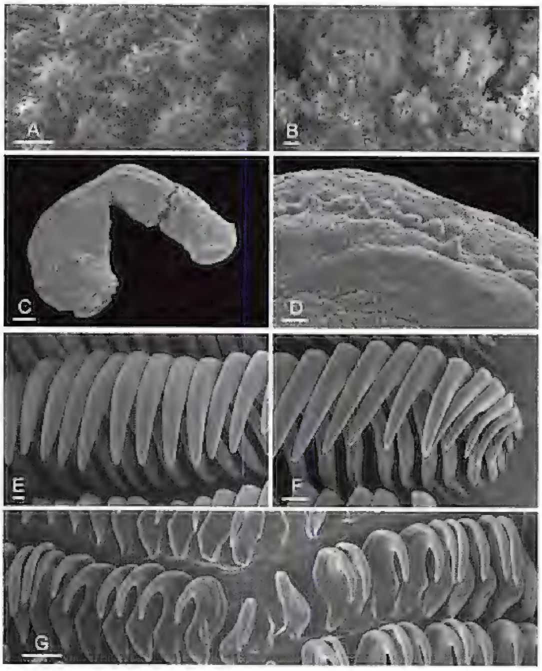

FIGURE 326. *Discodorididae rubra*, paratype of *Archidoris hawaiiensis*, BPBM 8920. A. Dorsal tubercles, scale = 100 μm.— B. Dorsal tubercles, scale = 20 μm.— C. Penis, scale = 100 μm.— D. Penis, detail, scale = 20 μm.— E. Median teeth, scale = 10 μm.— F. Outermost teeth, scale = 20μm.— G. Innermost teeth, scale = 30 μm.

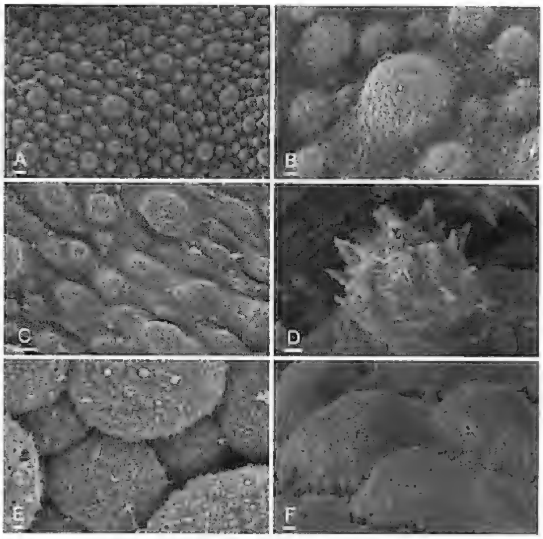

FIGURE 327. *Discodorididae rubra*, dorsal notum, tubercles. A. CASIZ 065782, scale = 100 μm.— B. CASIZ 065782, scale = 30 μm.— C. AM C124437, scale = 200 μm.— D. AM C124437, scale = 20 μm.— E. CASIZ 071238 (#1), scale = 20 μm.— F. CASIZ 087907, scale = 20 μm.

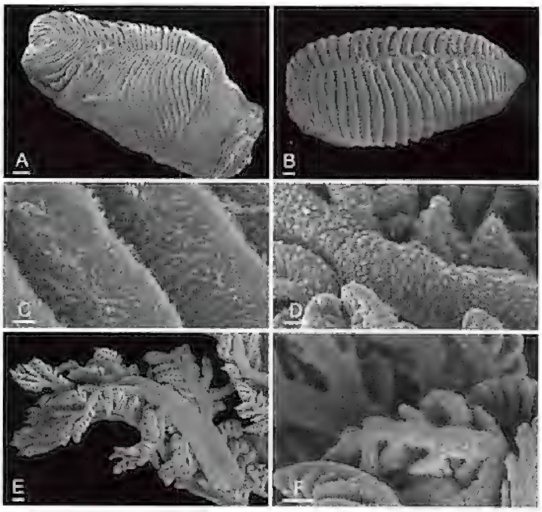

FIGURE 328. *Discodorididae rubra*, rhinophores and gills. A. Rhinophore, AM C124437, scale = 300 μm.— B. Rhinophore, CASIZ 071238 (#2), scale = 100 μm.— C. Rhinophoral lamellae, CASIZ 071238 (#2), scale = 30 μm.— D. Branchial plume, detail, CASIZ 065782, scale = 60 μm.— E. Branchial plume, CASIZ 071238 (#1), scale = 200 μm.— F. Branchial plume, detail, CASIZ 071238 (#1), scale = 100μm.

specimen (CASIZ 071238 #1), 22 × (50-0-50) in a 33 mm long specimen (CASIZ 065782), 23 × (60-0-60) in a 35 mm long specimen (CASIZ 086684), 23 × (65-0-65) in a 30 mm long specimen (CASIZ 071238 #2), and 24 × (75-0-75) in an 68 mm long specimen (CASIZ 087907), 25 × (60-0-60) in a 58 mm long specimen (CASIZ 081904), and 30 × (85-0-85) in a 110 mm long specimen (AM C124327). The rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant (although the median teeth are slightly larger than the other ones), except for the six or eight innermost teeth of which the size increases gradually and the six or eight outermost ones of which the size decreases gradually. All teeth are hamate, including the outermost ones, although the base of the last outermost tooth can be reduced. The teeth are not grooved, with no denticles.

Nervous system. The length of the circum-esophageal nerve ring varies but is short. It can

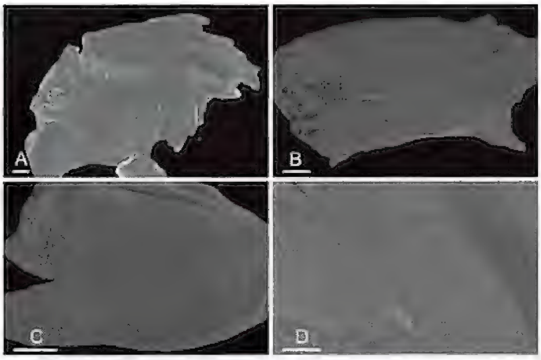

FIGURE 329. *Discodorididae rubra*, smooth labial cuticle. A. CASIZ 087907, scale = 200 µm.— B. CASIZ 071238 (#2), scale = 200 µm.— C. CASIZ 086684, scale = 200 µm.— D. CASIZ 065782, scale = 20 µm.

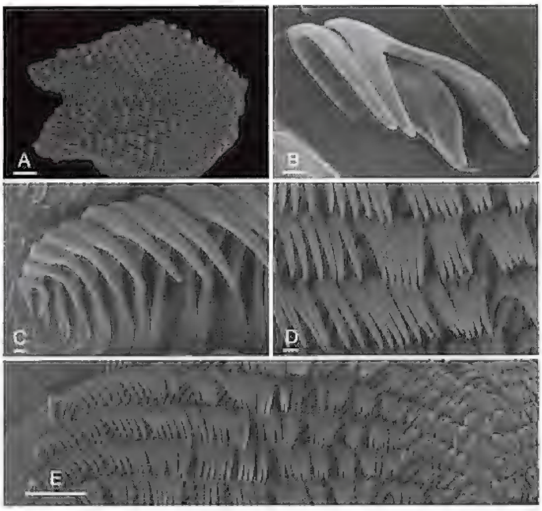

FIGURE 330. *Discodorididae rubra*, radula. A. CASIZ 065782, scale = 200 µm.— B. Innermost teeth, CASIZ 087907, scale = 10µm.— C. Outermost teeth, CASIZ 071238 (#2), scale = 10 µm.— D. Median teeth, CASIZ 071238 (#2), scale = 30 µm.— E. Left rows, CASIZ 071238 (#2), scale = 200 µm.

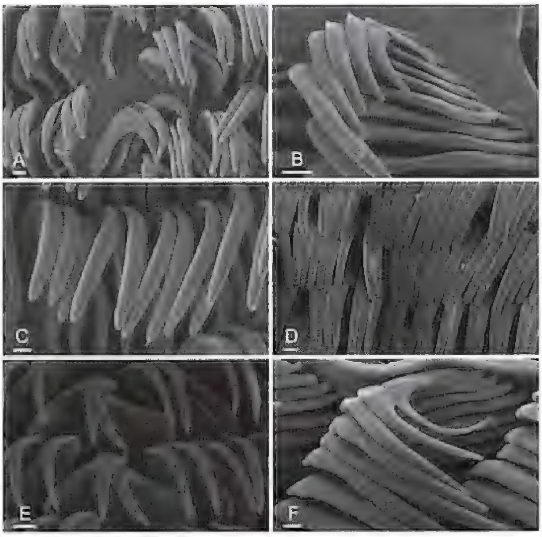

FIGURE 331. *Discodorididae rubra*, radula. A. Innermost teeth, CASIZ 086684, scale = 10 µm.— B. Outermost teeth, CASIZ 086684, scale = 20 µm.— C. Median teeth, CASIZ 086684, scale = 20 µm.— D. Median teeth, AM C124437, scale = 30 µm.— E. Innermost teeth, AM C124437, scale = 20 µm.— F. Outermost teeth, AM C124437, scale = 10 µm.

equal up to three times the width of the cerebropleural ganglia. The cerebral, pleural, and pedal ganglia are fused. Their surface is smooth.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is convoluted with several tight loops or only two loose loops (e.g., AM C124327). The division between male and female ducts (hidden by the female gland mass) could not be seen by dissection. The prostate is divided in a proximal whitish part and a distal yellowish-orange part. The deferent duct is convoluted and has several tight loops, although it is straight for the first half of its length. The deferent duct ends in a distinct penis. Its surface bears small conical papillae. Their shape, number, and position vary among specimens, but they are always present. Their apex is rounded or pointed. In most specimens, they alternate on each side of a longitudinal line. However, the penis of some individuals has two rows of papillae, and some have only one row. The vaginal duct can be straight, loosely or tightly convoluted. The fertilization duct can be straight and short or tightly convoluted with several loops. The connection between the fertilization duct and the female gland mass may or may not be marked by a clear duct. The duct of the receptaculum seminis is short. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is located underneath the receptaculum seminis. The bursa copulatrix can be as large as the receptaculum seminis or up to three times larger. The bursa copulatrix is spheri-

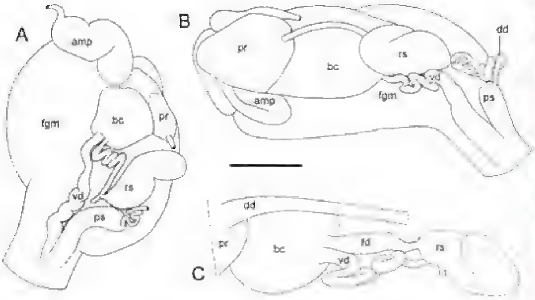

FIGURE 332. *Discodorididae rubra*, reproductive system. A. CASIZ 087907, scale = 1.3 mm.— B. CASIZ 071238 (#1), scale = 2 mm.— C. Spermatic pouches, CASIZ 071238 (#1), scale = 2 mm.

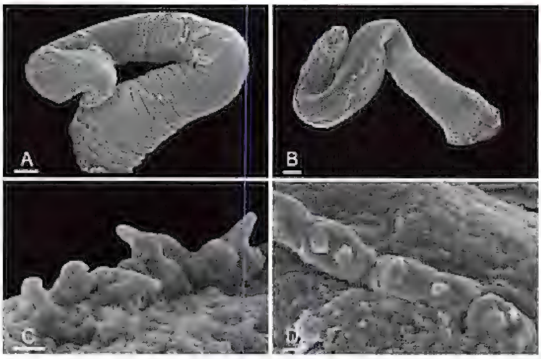

FIGURE 334. *Discodorididae rubra*, penis. A. CASIZ 081904, scale = 200μm.— B. CASIZ 086684, scale = 100 μm.— C. CASIZ 086684, scale = 10 μm.— D. CASIZ 086684, scale = 10μm.

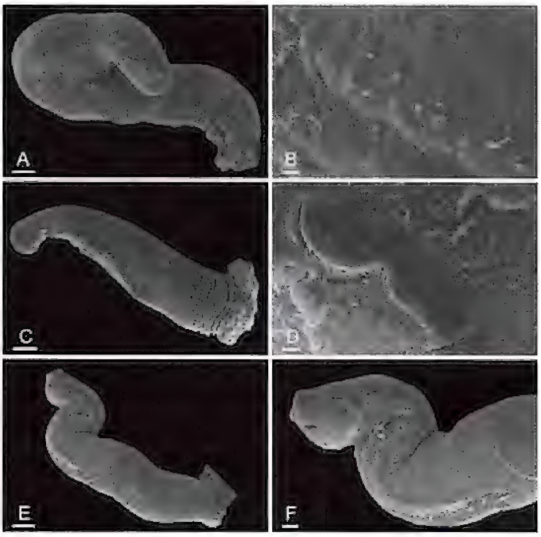

FIGURE 333. *Discodorididae rubra*, penis. A. CASIZ 065782, scale = 100 μm.— B. CASIZ 065782, scale = 10 μm.— C. AM C124437, scale = 200 μm.— D. AM C124437, scale = 20 μm.— E. CASIZ 087907, scale = 200 μm.— F. CASIZ 087907, scale = 100 μm.

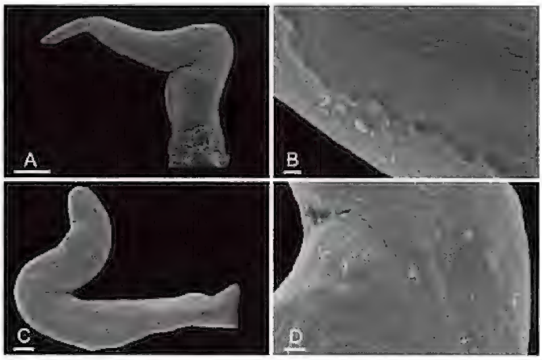

FIGURE 335. *Discodorididae rubra*, penis. A. CASIZ 071238 (#1), scale = 200 μm.— B. CASIZ 071238 (#1), scale = 20 μm.— C. CASIZ 071238 (#2), scale = 100 μm.— D. CASIZ 071238 (#2), scale = 20 μm.

cal-ovate and smooth. The receptaculum seminis is elongated, sausage-shaped, and, in most individuals, U-shaped.

DIAGNOSTIC FEATURES.— The color of the dorsal notum is diagnostic of *rubra*. In particular, the black spots at the apex of some white tubercles remain distinguishable in most preserved specimens. The penis of *rubra* is also typical and can hardly be confused with the penis of other species. Some additional anatomical characters may help confirm the identification, such as the sausage-shape and U-shaped receptaculum seminis, and a deferent duct straight for the first half of its length and then convoluted for its second half.

DISCUSSION.— Anatomical and morphological information available in the two original descriptions is largely congruent with the description provided here. The largest animals known are 110 mm long preserved. However, the radular formula provided by Bergh for *rubra* needs to be commented on. The number or rows (44) described by Bergh is significantly higher than the number of rows of all the other radulae known (22 rows in the original description of *hawaiiensis*, and from 16 to 30 rows in the present study). This difference can hardly be explained by the size of the specimens because the individual dissected by Bergh was 75 mm long, and the individual dissected by Kay and Young was 110 mm long. The number of teeth per half row (105) described by Bergh also is quite high. This suggests that the radular formula of *rubra* does vary among specimens. Future workers may need to pay close attention to this character.

SUPRA-SPECIFIC RELATIONSHIPS.— Terry Gosliner (Bill's Rudman Sea Slug Forum, 28 September 2002, #8051) proposed to classify *rubra* in *Peltodoris* because of its lack of jaw elements. However, a new phylogenetic test of the relationships of *rubra* confirms that it does not belong to the clades *Discodoris* and *Peltodoris*, but rather is part of a large metaphyletic group at the base of *Discodorididae* (see Dayrat and Gosliner 2005). The Linnaean binomial should be "*Montereina*" *rubra*. Possible names under the *ICPN* are "*Montereina*" *rubra* and *Discodorididae rubra*.

FUTURE STUDIES.— As always, it would be interesting to determine whether the individual variation observed in the penial morphology is infra-specific or the indication of cryptic species.

"*Montereina*" *sandiegensis* (Cooper, 1863) New combination
Discodorididae sandiegensis (Cooper, 1863)

Figures 336-337.

Doris (*Actinocyclus*?) *sandiegensis* Cooper, 1863:204-205.
Doridopsis sandiegensis.— Abraham, 1877:240.
Diaulula sandiegiensis [for *sandiegensis*].— Bergh, 1878b:567.
Discodoris sandigensis.— Bertsch, 1980:224.
Discodorididae sandiegensis.— Dayrat and Gosliner, 2005:205.

TYPE MATERIAL.— The type material could not be found. It probably is lost.

TYPE LOCALITY.— San Diego Bay, California.

ADDITIONAL MATERIAL DISSECTED.— **California**, San Francisco Estuary, Angel Island, 1 November 1975, one specimen 40/40 mm preserved, leg. Carlton, Chaffee, and Bowman, identified as *Diaulula sandiegensis* by unknown identifier (CASIZ 131361); California, MontereyBay, Pacific Grove, [no collecting date], one specimen 55/35 mm preserved, leg. F. MacFarland, identified as *Diaulula sandiegensis* by F. MacFarland (CASIZ 068279); **Alaska**, Aleutian Islands, 4 July 1994, two specimens 50/35 (#1) [dissected] and 30/20 (#2) mm preserved, leg. Roger Clark, aboard F/V Vesteraader, identified as *Diaulula sandiegensis* by T. M. Gosliner (CASIZ 106537).

DISTRIBUTION.— Northeastern Pacific: from Aleutian Islands, Alaska to Cabo San Lucas, Baja California (McDonald 1983). Mentioned in Japan as well (Baba 1957)

OCCURENCE.— It is a common species in rocky intertidal (McDonald 1983).

HABITAT.— Rocky shore, occasionally in sloughs and sometimes on docks and pilings in bays. Feeds on sponges, such as *Halichondria* and *Haliclona* (McDonald 1983).

LITERATURE.— The literature on *sandiegensis* is abundant: It is a common species on the northeastern Pacific Coast, and many authors recorded its presence and commented on its color or external morphology (McDonald 1983). The infra-specific variation of several features, such as the dorsal color and the radular formula, is well known. Anatomical data can be found in several contributions (McDonald 1983, including MacFarland (1897, 1906, 1966), O'Donoghue (1921, 1927), and Valdés and Gosliner (2001).

REMARKS ON THE ORIGINAL DESCRIPTION.— The original description was probably based on more than one specimen because Cooper mentions that there are "numerous [animals] among grass on mud flats in San Diego Bay." However, Cooper does not give any precise number. For the size, Cooper gives 90/65 mm, likely for live animals. The original description is brief: "Pale brownish yellow, with large annular brown spots irregularly scattered, ranging from twelve to twenty, or entirely brown. Surface slightly rough, sometimes a little tuberculated. Dorsal tentacles [i.e., rhinophores] conical, retractile; branchiae large, rising in five parts which become tripinnately divided, expanding so as to cover the posterior third of the body like an umbrella. Mouth, proboscidiform, with two short lateral tentacles." The internal anatomy was not described.

Description of new specimens (Fig. 337).— *Color*. No data on the live color of the animals dissected here was available. Preserved specimens have a whitish dorsal notum, with a few traces or dark rings.

External morphology. The body is oval. Its length equals less than twice its width. The foot is rounded posteriorly and anteriorly. The width of the foot equals about one half of the width of the dorsal notum. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, not grooved. The dorsal notum is covered with caryophyllidia. In preserved specimens, the margins of the rhinophoral and branchial sheaths can be smooth or crenulate. The margin of the gill opening is not star-shaped with five lobes. There are six multipinnate branchial plumes arranged in circle around the anus. The rhinophores have from 15 to 25 lamellae.

Digestive system. The stomach tends to be narrow, free, and median (i.e., embedded on its two lateral sides by the digestive gland). A caecum is located on the left posterior side of the stomach. The labial cuticle is smooth. The radular sac cannot be seen by dorsal dissection. The radula formula is 21 × (28-0-28) in a 50 mm long specimen (CASIZ 106537 #1). The rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the five to ten innermost teeth of which the size increases gradually and the last four to six outermost ones of which the size decreases gradually. All teeth are hamate, including the outermost ones. The teeth bear no denticle.

Nervous system. The circum-esophageal nerve ring is short: its length equals between one and two times the width of the cerebro-pleural ganglia. The cerebral and pleural ganglia are fused.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is convoluted, with several tight loops. The division between male and female ducts (in the female gland mass) could not be seen by dissection. The prostate is divided in a proximal whitish part and a distal yellowish part. The deferent duct is very long, convoluted, with many tight loops. No distinct, permanent, penial structure was found. The vaginal duct is straight. The fertilization duct is also short, almost straight. The connection between the fertilization duct and the female gland mass is marked by a clear duct. The disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) is located underneath the receptaculum seminis. The bursa copulatrix is much larger than the receptaculum seminis (up to ten times). Both pouches are spherical-ovate, with a smooth surface.

Diagnostic features.— The best way to identify *sandiegensis* is its dorsal color (Fig. 336). Although they vary in size and position, the brown or black rings (or occasionally blotches) are diagnosic. Internal features are more problematic because many species have a long deferent duct (e.g., *Discodorididae nobilis*, with a similar geographic distribution), and the latter is hardly diagnostic.

Infra-specific character variation.— The individual variation of the dorsal color was efficiently summarized by McDonald (1983): background from white to chocolate brown, but commonly pale cream to raw amber; almost black or dark brown rings (or occasionally irregular blotches) which vary in size, number and position (most commonly arranged in two longitudinal rows on either side of the median line, with 3 or 4 rings each); some specimens can lack the dorsal rings, and some specimens can be darker. The maximum size reported is 150 mm (McDonald 1983). All radular formulae found in the literature fit within this range of variation: 13/23 × (25/34-0-25/34) (McDonald 1983).

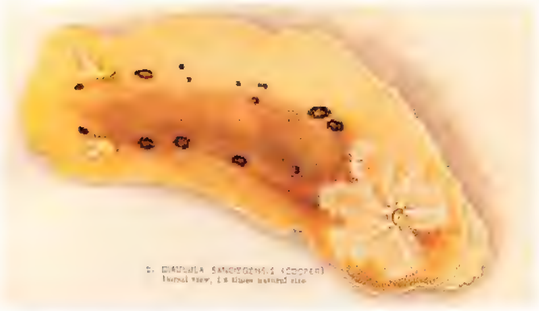

FIGURE 336. *Discodorididae sandiegensis*, dorsal view (MacFarland 1906: plate XXIII, fig. 5).

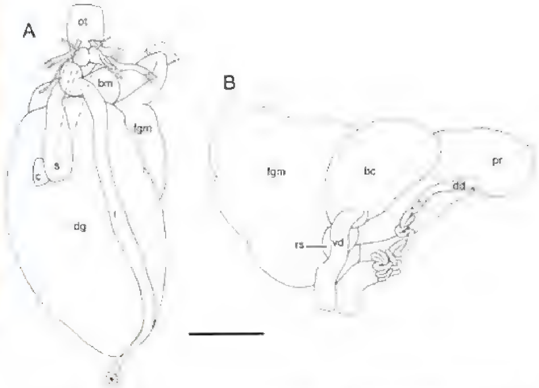

FIGURE 337. *Discodorididae sandiegensis*, CASIZ 068279. A. General anatomy, scale = 8 mm.— B. Reproductive system, scale = 4.5 mm.

DISCUSSION.— The taxonomy of *sandiegensis*, as a species, is interesting because it is unclear whether or not the Japanese specimens (Baba 1957) are really part of the same entity as the specimens from northeastern Pacific coast, and because there is a large variation in the dorsal color, especially in the northern part of the range (McDonald 1983). It would be interesting to study the population structure of this species, from Mexico up to northwestern Pacific, and address whether there are one or more than one species.

SUPRA-SPECIFIC RELATIONSHIPS.— Clearly, *sandiegensis* does not belong to *Actinocyclus*, as originally suggested by Cooper (1863), and it does not belong either to *Doriopsis*, as suggested by Abraham (1877). Most authors classified *sandiegensis* in *Diaulula*, although a few authors (e.g., Bertsch 1980) re-allocated it to *Discodoris*.

A phylogenetic test of the relationships of *sandiegensis* shows that it does not belong to the clade *Discodoris*, but rather is part of a large metaphyletic group at the base of *Discodorididae*. As a result, *Diaulula* is not a clade. The Linnaean binomial should be "*Montereina*" *sandiegensis*. Possible names under the *ICPN* are "*Montereina*" *sandiegensis* and *Discodorididae sandiegensis*.

"*Montereina*" *sauvagei* (Rochebrune, 1881) New combination
Discodorididae sauvagei (Rochebrune, 1881) New combination

Figure 338.

Peltodoris sauvagei Rochebrune, 1881:263, plate 18, fig. 6.— Rochebrune, 1882b:28.
Discodoris sauvagei.— Ortea et al., 1998:109-114, plate 1, fig. 1.

TYPE MATERIAL.— The holotype, by monotypy, was not found at the MNHN, where, according to the original publication, it was deposited. It is probably lost. It was collected by Mr. de Cessac, in 1874 (Rochebrune 1882b:24).

TYPE LOCALITY.— Ile Sainte-Lucie, Cape Verde Islands.

DISTRIBUTION.— This species is only known from the Cape Verde Islands, from the holotype and four additional specimens described by Ortea et al. (1998).

HABITAT.— Under rocks in the intertidal zone (Ortea et al. 1998).

REMARKS ON THE ORIGINAL DESCRIPTION (Fig. 338).— There is not much to discuss in the original description because it is quite short. However, the drawing of the dorsal color of the live animal (probably drawn in Paris, based on de Cessac's field notes), is informative: grey-greenish dorsal background, with yellowish gills and purple rhinophores; grey inferior side. The size of the preserved animal was 22/15 mm. The dorsal notum was covered with small tubercles ('granulations') that could only be seen with a scope. Note that the brief note published by Rochebrune (1882b) is just an extract from the original description.

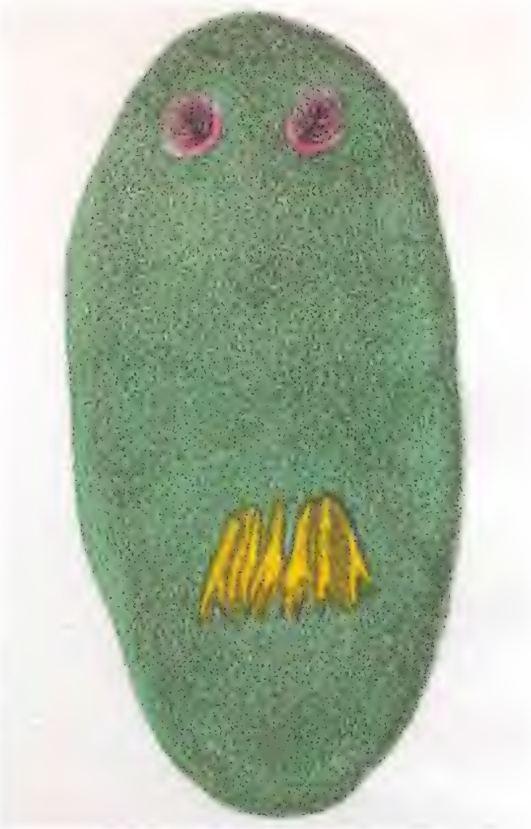

FIGURE 338. *Discodorididae sauvagei*, illustration from original description (Rochebrune 1881: plate 18, fig. 6).

DISCUSSION.— In the original description, Rochebrune (1881) compared *sauvagei* with what he called *Peltodoris crucis* (now *Discodorididae crucis*) from the West Indies. These two species are likely different. The color of *sauvagei* is distinct. This color was used by Ortea et al. (1998) to re-identify new specimens of *sauvagei* from the Cape Verde Islands. Their additional specimens fit perfectly the original description. Ortea and co-authors added a few morphological and anatomical data. A few of them are emphasized here. The maximum length was 80 mm, alive, which suggests that the holotype described by Rochebrune probably was a young individual. The dorsal tubercles are not caryophyllidia. The anterior foot is bilabiate with a notched upper lip. The labial cuticle is armed with a pair of jaws (which led Ortea and co-authors to re-allocate *sauvagei* from *Peltodoris* to *Discodoris*). The radular formula is 28 × (61-0-61) in an 80 mm long specimen, alive, and 25 × (50-0-50) in a 70 mm long specimen, alive. The teeth are hamate, with no denticles. Unfortunately, the reproductive system was only briefly described by Ortea and co-authors. However, they mentioned that 'el pene es inerme,' which suggests that there is no permanent, distinct copulatory organ.

The color of *sauvagei* is distinct. No other names was found that would apply to the same entity. However, many species have only been described based on dead, preserved specimens, including several species from the Caribbean Sea: synonyms may be discovered when we know more about the color of live animals of those species.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *sauvagei* shows that it does not belong to the clades *Discodoris* or *Peltodoris*, but rather is part of a large metaphyletic group at the base of *Discodorididae*. The Linnaean binomial should be "*Montereina*" *sauvagei*. Possible names under the *ICPN* are "*Montereina*" *sauvagei* and *Discodorididae sauvagei*.

"*Montereina*" *sibogae* (Bergh, 1905) New combination
***Discodorididae sibogae* (Bergh, 1905) New combination**

Figure 339.

Anisodoris sibogae Bergh, 1905:96-97, plate III, fig. 11, plate XIII, fig. 31-33.

Type material.— Three syntypes (ZMA Moll 3.05-144-145): two specimens [one syntype is probably lost] 32/22 (#1) and 26/18 (#2) mm preserved, leg. Siboga Expedition, 26 October 1899.

Type locality.— Saleyer anchorage and surroundings (Siboga station 213), 36 meters maximum depth (trawl, townet), including Pulu Pasi Tanette, near the northern point of Saleyer Island [or Selayar, Celebes, Indonesia].

Type material condition.— One syntype, probably entirely dissected by Bergh, is missing. One syntype is complete and well preserved externally. The third and last syntype was opened by Bergh: the reproductive system is missing, but the radula, the labial cuticle and the rest of the digestive system remain. The gills (6 tripinnate plumes) are largely destroyed in both syntypes.

Distribution.— The syntypes are the only specimens known.

Habitat.— Coral reef, mud, and mud with sand.

Remarks on the original description (Fig. 339).— One live animal measured 38/20 mm, and had a brownish-yellow dorsal notum covered with knob-like tubercles. The two specimens are currently homogeneously white. The preserved specimens observed by Bergh would range from 26 to 43 mm in length. The dorsal tubercles look like the large tubercles found in *Carminodoris* species. In one syntype, they have a flattened apex, which could be due to preservation. Bergh's description is not informative: it mainly includes measurements.The oral tentacles of the two syntypes examined are digitiform and that the anterior foot is bilabiate with an upper lip notched. Fifteen rhinophoral lamellae were found in the syntype #1 (they could not be counted in the syntype #2). Bergh mentioned five branchial plumes. The radular formula given by Bergh was 26 × (65-0-65), with smooth, hamate teeth. There is no distinctive feature in the reproductive system, except for a 1.5 mm long penis.

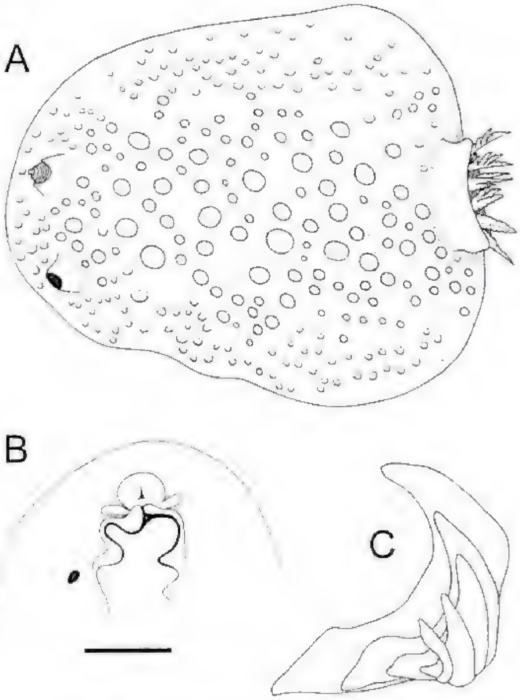

Figure 339. *Discodorididae sibogae*, syntypes. A. Dorsal view, syntype #2, total length = 26 mm (preserved).— B. Anterior, ventral view, syntype #2, scale = 5 mm.— C. Outermost teeth, syntype dissected by Bergh and probably lost, after Bergh (1905: plate XIII, fig. 33), scale = 5 mm.

Discussion.— The syntype that is still complete was not dissected because no other (non-type) specimens was available. This syntype is left for a future worker who will really need to dissect it. New specimens from the type locality would certainly help address the status of *sibogae*. The fact that we have an idea of its color and external shape should help its identification.

Supra-specific relationships.— A phylogenetic test of the relationships of *sibogae* shows that it does not belong to the clades *Anisodoris*, but rather is part of a large metaphyletic group at the base of *Discodorididae*. The Linnaean binomial should be "*Montereina*" *sibogae*. Possible names under the *ICPN* are "*Montereina*" *sibogae* and *Discodorididae sibogae*. It could belong to *Carminodoris*, but this is largely speculative and would need to be addressed through dissection.

"*Montereina*" *sordii* (Perrone, 1990) New combination
Discodorididae sordii (Perrone, 1990) New combination

Peltodoris sordii Perrone, 1990a:296-299, figs 1-8.
Discodoris sordii.— Cattaneo-Vietti et al., 1990:19.

Type material.— Holotype (Stazione di Biologia Marina di Porto Cesareo, Università di Lecce), by original designation: one specimen 25/11 mm alive, leg. A. Perrone, September 1986. One paratype (not deposited): one specimen 20/10 alive. The type material could not be borrowed despite several requests. Two letters sent to the Stazione di Biologia Marina di Porto Cesareo remained unanswered, as well as a letter sent to Antonio Perrone's personal address. The types are not publicly available.

Type locality.— Porto Cesareo (Lecce), 3 meters depth, Golfo di Taranto, Mediterranean.

Etymology.— This species was dedicated to Prof. Mauro Sordi, in memory of his work on nudibranchs from the Thyrrenian Sea.

Distribution.— This species is only known from the two type specimens.

Remarks on the original description.— The original description of *Peltodoris sordii* is the perfect illustration of what taxonomy should not be. The content of this description is so poor that the author does not even provide a complete radular formula (the author simply indicated that it contained 18 rows of teeth). A few features are mentioned here: live animals were purple, with some red and brown tints as well; the tubercles did not seem to be caryophyllidia; the oral tentacles seem to be digitiform; the labial cuticle was smooth; all teeth (of the 18 rows) were hamate and identical, which suggests that outermost teeth were not denticulate or pectinate; the brief description of the reproductive system is useless (no penial morphology was mentioned).

Discussion.— This kind of work, which was acceptable in the 1850s, was unacceptable in the 1990s. Reviewers and editors should not have accepted this new species description. Unfortunately, taxonomic rigor forces us to take into account all available names, which, in a case like *sordii* is a waste of time. Perrone compared *sordii* with two other species, *Discodoris maculosa* (here called *Tayuva lilacina*) and *Discodoris planata*. Given the purple-reddish color of the dorsal notum, *sordii* is probably not another name for *Tayuva lilacina*. The differences between *sordii* and *Geitodoris planata* mentioned by Perrone are not convincing: "*Peltodoris sordii* can be distinguished easily from *Discodoris planata* (Alder & Hancock, 1846) (= *Discodoris stellifera* Vayssière, 1904) because the notum and the dorsal tubercles have different structures; also the anatomical comparison of the internal organs is sufficient to establish numerous differences." (Perrone 1990a:299, translated here) The color of the dorsal notum suggests that *sordii* might just be a junior synonym of *Geitodoris planata* (Alder & Hancock, 1846). In any case, *Peltodoris sordii* is regarded as a *nomen dubium* because its original description is largely incomplete and because the types (especially the holotype) are not publicly available. Maybe future workers will have more luck.

Supra-specific relationships.— Cattaneo-Vietti et al. (1990) mentioned *sordii* in a list of Mediterranean nudibranch species, and re-allocated it into *Discodoris* with no justification. A phylogenetic test of the relationships of *sordii* shows that it does not belong to the clades *Peltodoris* and *Discodoris*, but rather is part of a large metaphyletic group at the base of *Discodorididae*, largely because of lack of sufficient data. The Linnaean binomial should be "*Montereina*" *sordii*. Possible names under the *ICPN* are "*Montereina*" *sordii* and *Discodorididae sordii*.

"*Montereina*" *tristis* (Bergh, 1899) New combination
Discodorididae tristis (Bergh, 1899) New combination

Discodoris tristis Bergh, 1899:11-14.

Type material.— The holotype, by monotypy, could not be found. It is neither at the MNHN, nor at the ZMUC. However, it could be in Monaco because the material described by Bergh came from an expedition sponsored by the Prince of Monaco. My letter to the Musée océanographique de Monaco was not answered.

Type locality.— According to the original publication, Ponta Delgada, Azores, [eastern Atlantic Ocean].

Distribution.— So far, *tristis* is only known from the type locality.

Remarks on the original description.— The size of the preserved individual was 45/20 mm. The ground color of its dorsal notum was dark brown-greyish with gills slightly lighter and sprinkled with black dots. Rhinophores had a yellow tip. The hyponotum was grey-whitish, but covered with small purple-grey dots. The color of the foot sole was similar to that of the hyponotum, but the dots were larger and tighter. The notum was covered with tubercles, small and tight, hemispherical or conical, and filled with long spicules. The anterior foot was bilabiate with the superior lip notched. More importantly, the oral tentacles were a little flattened, with an outer longitudinal groove. The branchial pocket was round, but its margin was divided in four lobes. The latter are described as "assez forts," which literally means 'quite strong.' There were six branchial plumes. The labial cuticle was armed with jaw rodlets. The radular formula was 34 × (46-0-46) in a 45 mm long specimen, with simply hamate teeth. No denticles were mentioned by Bergh. The description of the reproductive system is hardly helpful because of the absence of drawing. In any case, Bergh mentioned a large prostate, a 2 mm long penis, a spherical bursa copulatrix (7.5 mm in diameter), and a pear-shaped receptaculum seminis (2mm long). He did not mention any vaginal or vestibular spines. Nor did he mention any accessory glands.

Discussion.— The re-identification of *tristis* is quite difficult because the type could not be found and because Bergh did not publish any drawings. However, two important features help: a lobed branchial pocket, and oral tentacles with a longitudinal groove. Grooved oral tentacles are uncommon in discodorids: they are found in *Paradoris* and *Platydoris*. *Paradoris* species are characterized by a narrow radula (with the number of rows exceeding the number teeth per half row), and it seems that *tristis* belongs to *Paradoris*. However, the branchial pocket of *Platydoris* species is deeply lobed, which is compatible with Bergh's description of *tristis*. Therefore, *tristis* could be one of the nominal species of *Platydoris*.

It could be a synonym of *Platydoris argo*, recorded from the Azores (Wirtz and Martins 1993; Wirtz 1998). This remains hypothetical, however, because it would imply that, first, Bergh missed the vaginal spines, and, second, that he did not recognize that this specimen was a *Platydoris*, although he seems to have made this mistake with *Discodoris sibogae* Bergh, 1905, likely a synonym of *Platydoris scabra* (Cuvier, 1804). In conclusion, *tristis* is regarded as a *nomen dubium*, although it could just be a synonym of *Platydoris argo*. Note that Marcus and Marcus (1967a) briefly mentioned *tristis* without adding any material or commenting on it (they simply noticed the grooved oral tentacles).

Supra-specific relationships.— A phylogenetic test of the relationships of *tristis* did not confirm that it belongs to *Platydoris* (see analyses #20 and #21), which is probably related to the lack of sufficient data: *tristis* belongs to *Discodorididae*, but it is unclear whether or not it belongs to *Platydoris*.

"*Montereina*" *voniheringi* (MacFarland, 1909) New combination
Discodorididae voniheringi (MacFarland, 1909) New combination

Figure 340.

Discodoris voniheringi MacFarland, 1909:73-82, plates XIII-XV, figs 66-76.

Type material.— Holotype (CASIZ 021022, including five slides), by original designation: one specimen 13/9 mm preserved, leg. A. W. Greeley, 20 July 1899. This was formerly the type No. 147, Invertebrate Series, Leland Stanford Junior University Zoological Museum.

Type locality.— Riacho Doce, Alagoas, Brazil.

Type material condition.— The holotype, dissected by MacFarland, probably dried for a while: it is now dark, shapeless, destroyed, and useless. Some tubercles on the surface of the dorsal notum do not seem to be caryophyllidia. The five slides include: the radula and the jaws; some histology of the reproductive system; one salivary gland; some histology of the prostate gland; and another structure that could be the penial papilla. The radula, described in detail by MacFarland, can hardly be observed now because the slide is completely dry. The slide labeled (not by MacFarland) "penis ?" could hold the unarmed penial papilla, but this is uncertain.

Distribution.— The type is the only specimen known.

Literature.— Information about *voniheringi* can only be found in the original description. Marcus and Marcus (1967a) briefly mentioned the existence of *voniheringi* in a list of Atlantic *Discodoris* species.

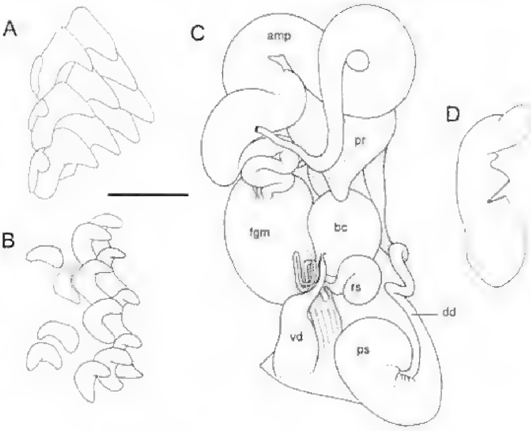

Figure 340. *Discodorididae voniheringi*, holotype, CASIZ 021022. A. Outermost teeth, slide, as currently preserved, scale = 100 µm.— B. Innermost teeth, slide, as currently preserved, scale = 75 µm.— C. Reproductive system, from MacFarland (1909: fig. 74).— D. Organ on slide labeled as "penis ?", scale = 0.7 mm.

Remarks on the original description (Fig. 340).— The original description of *voniheringi* is quite long. Some of the most important features are discussed here. The animal measured 20/14.5 mm when MacFarland observed it. It is much smaller now (probably because it dried for a while). The dorsal color is described only from the preserved specimen, which means that it may not correspond at all to the live animal: "pinkish gray, sprinkled everywhere with minute dark brown, or black spots." MacFarland described some tubercles on the dorsal notum. However, nothing suggests that he saw caryophyllidia. The type is currently so shapeless that it is hardly helpful. The anterior foot is bilabiate, with a notched upper lip. The oral tentacles are digitiform. There are 25 rhinophoral lamellae, six branchial plumes. The labial cuticle is unusual. It consists of two lateral plates, and one median plate, the three of them being covered with "very short blunt rodlets measuring up to 0.002 mm in diameter, and approximately the same in height." So far, only *Paradoris* species were found to have three jaw plates. However, the third jawplate described by MacFarland is different from the third jaw plate in *Paradoris*. In the latter, the third jaw plate is larger than long, whereas the third jaw plate described in *voniheringi* is much longer than it is large. The radular formula is 26 × (46/50-0-46/50). This formula can hardly be checked because of the poor condition of the slide, but it seems that there might be more than only 26 rows. Teeth are simply hamate, with no denticles. The reproductive system was also thoroughly described. It is possible, based on the size of the female gland mass (called 'nidamental-albumen gland complex' by MacFarland) compared to other organs, that the specimen was not fully mature. In any case, the deferent duct and the vaginal duct are particularly long. In fact the vaginal duct is straight. The fertilization duct, however, is long and convoluted. The penis is "bluntly cylindrical in shape, slightly tapering and is entirely destitute of any armature." MacFarland did not give the length of this penis: if the slide labeled "penis ?" contains the penis, then the latter is less than 2 mm long.

Discussion.— MacFarland did not compare *voniheringi* to any other existing *Discodoris* species, and did not mention any diagnostic feature that could help identify it. He simply wrote that it was "clearly different from any hitherto described," which is quite brief. Without any information about the dorsal color of the live animal, without any potentially diagnostic, radular characters (such as denticles), and without any peculiar armature on the penis, etc., it will be difficult to re-identify this species, even with specimens from the type locality. A long fertilization duct is hardly diagnostic of any species because it is common in discodorids. However, MacFarland was correct about the fact that *voniheringi* belongs to *Discodorididae*. Nonetheless, *voniheringi* MacFarland, 1909 is regarded as a *nomen dubium* here.

Supra-specific relationships.— A phylogenetic test of the relationships of *voniheringi* shows that it does not belong to *Discodoris*. It is just part of a large metaphyletic group at the base of *Discodorididae*. The Linnaean name should be "*Montereina*" *voniheringi*. Possible names underthe *ICPN* are "*Montereina*" *voniheringi* and *Discodorididae voniheringi*.

"*Montereina*" *worki* (Marcus and Marcus, 1967) New combination
Discodorididae worki (Marcus and Marcus, 1967) New combination

Figures 341-343.

Anisodoris worki Marcus & Marcus, 1967a:66-70, figs 85-89.— Marcus & Marcus, 1970a:62.— Redfern, 2001:176, plate 119, fig. 726.

Type material.— Holotype (NMNH 576289, slides F849, F850), by original designation: one specimen 18/10 mm preserved [according to the original description, the live animal measured 28.5/16 mm], leg. Bayer [leg. R.C. Work according to the original description], 7 August 1964.

Type Locality.— [East end of County (MacArthur) Causeway], Biscayne Bay, Florida.

Type material condition.— The holotype was entirely dissected by Eveline and Ernst Marcus. Parts of the body wall (dorsal notum and foot) remain. The reproductive system, the radula, and the labial cuticle, are preserved on slides. The slide with the radula and the labial cuticle, however, is in poor condition (the mounting solution is dry). Eveline and Ernst Marcus described the dorsal color of the live animal from a picture that was not found at the NMNH.

Additional material dissected.— Florida, Virginia Key, Norris Cut, off Miami, one specimen 35/23 preserved, 1 March 1966, leg. R. Work, donated by the University of Miami, identified as *Anisodoris worki* by an unknown identifier (NMNH 836766).

Distribution.— So far, three specimens of *worki* were collected from Florida (Marcus and Marcus 1967a, 1970a), including two specimens from the type locality (Biscayne Bay), one specimen was collected from Curaçao (Marcus and Marcus 1970a). One specimen was tentatively (but probably rightly) identified as *worki* by Redfern (2001) from the Bahamas. One can expect to find *worki* in the rest of the Caribbean Sea.

Habitat.— The holotype was found under rocks, and the additional specimen described here (USNM 836766) was found under intertidal rocks.

Remarks on the original description (Figs. 341A-C, E, G).— The live animal was yellowish, with dark spots in the connective tissue, except for the papillae, lighter than the spots; the middle of the dorsal notum is darker. The color of preserved specimens is whitish, with a few fuzzy darker spots; the middle of the back is still darker than the edges, and the black spots are interrupted by the papillae that are whitish. A few large dark spots are still present on the hyponotum. The foot is rounded posteriorly and anteriorly. The "cauliflower-like" organization of the dorsal tubercles, which are not caryophyllidia, is easily recognizable: a large tubercle is surrounded by smaller tubercles. All tubercles are rounded, not conical. There are between 15 and 20 rhinophoral lamellae. The upper lip of the anterior foot is notched. The digitiform oral tentacles are not grooved. The stomach is not embedded within the digestive gland. The labial cuticle is smooth. The slide on which the labial cuticle is preserved is in poor condition and the Marcus' observations could not be checked. Eveline and Ernst Marcus described a radular formula of 27 × (38-0-38). The slide on which the radula is preserved is in poor condition and the number of rows and teeth per half row could not be determined, although it seems that there are slightly fewer rows and teeth per half row. All teeth seem to be smooth. The distal vaginal gland described in the original description was observed on one of the slides. However, the muscular duct and the papillae ("with spikelets," i.e., probably small spines) of this gland as well as the penis were missing. The penis is actually coiled at its apex.

Description of an additional specimen (NMNH 836766, Figs. 341D, F, H-I, 342-343).— *Color*. The dorsal color of the preserved animal is homogeneously whitish. The hyponotum bears a few black dots. No information is available on the color of the live animal.

External morphology. The body is oval. The length equals less than twice the width. The anterior margin of the foot is bilabiate and the upper lip is notched. The oral tentacles are digitiform, not grooved. The notum is covered with the same tubercles as the holotype (large tubercles surrounded by smaller ones). All tubercles are densely filled with spicules. Small holes (diameter < 10 µm) and tufts of cilia on the dorsal notum are probably present but could not be observed. The margins of the rhinophoral sheaths and branchial pockets are crenulate. There are about 20 rhinophoral lamellae. There are six tripinnate gills arranged in circle around the anus.

Digestive system. The stomach is free. The intestine is straight and dorsal. The labial cuticle is smooth. The radular sac cannot be seen by dorsal dissection. The radular formula is 20 × (30-0-30) in a 35 mm specimen. Rachidian teeth are absent and the rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the first six or seven innermost ones (their size gradually increases) and the last four outermost

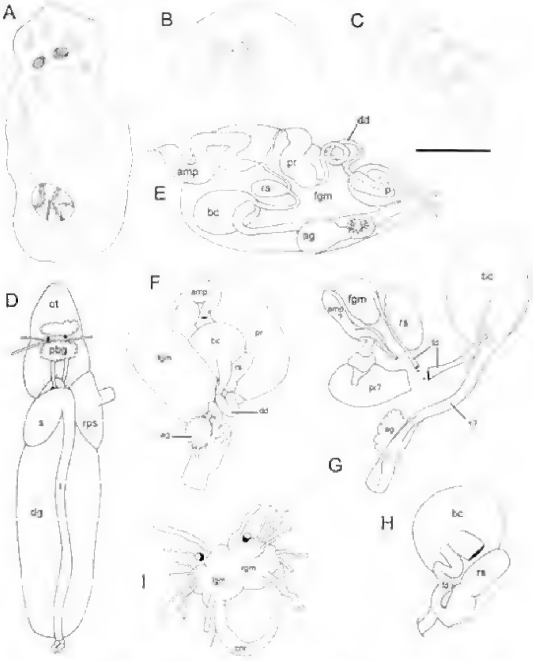

FIGURE 341. *Discodorididae worki*. A. Dorsal view, holotype, NMNH 576289, total length = 18 mm.— B. Anterior, ventral view, holotype, total width = 9 mm.— C. Outermost lateral radular teeth, holotype, as currently preserved on slide F850, scale = 60 µm.— D. General anatomy, NMNH 836766, scale = 6 mm.— E. Reproductive system, holotype, after Marcus and Marcus (1967a: fig. 88).— F. Reproductive system, NMNH 836766, scale = 2.5 mm.— G. Reproductive system, holotype, as currently preserved on slide F849, scale = 2.5 mm.— H. Spermatic pouches, NMNH 836766, scale = 1.5 mm.— I. Nervous system, NMNH 836766, scale = 1 mm.

ones (their size gradually decreases). All the teeth are simply hamate. The outermost tooth can be reduced. In some rows, the first innermost tooth can be coiled upon itself. This could just be an artifact. The teeth bear no denticles.

Nervous system. The length of the circumesophageal nerve ring equals about twice the width of the dorsal cerebro-pleural ganglia. The cerebral and pleural ganglia can be distinguished from one another. There are two blood glands, one anterior and one posterior to the cerebral ganglia.

Reproductive system. It is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is convoluted, with a few loops. The division between male and female ducts could not be seen by dissection. The prostate is divided in two white parts, hardly distinguishable. The proximal part of the deferent duct is wide and seems to be folded, as in *Tayuva*. The deferent duct joins a penial sheath that covers a smooth penis with a coiled apex. The vaginal duct is straight from the atrium to the bursa copulatrix. The latter is about three times larger than the receptaculum seminis, which is sausage-shaped. The fertilization duct is short, lightly convoluted (with two loops) from the bursa copulatrix to the female gland mass. The duct of the receptaculum seminis is short. There also is an accessory vaginal gland with a granular surface and a duct that opens into the vagina. This duct ends into a conical spine. It could not be determined whether or not this spine is hollow, but it likely is. In SEM, it seemed to be solid, but it might be because its apex was not clean. In any case, it corresponds to the big 'spikelet' mentioned in the original description.

Diagnostic features.— Marcus and Marcus (1970a) consider that several characters should help re-identify *worki*: the vaginal accessory gland and its 'spikelets,' the long penial papilla, and the cauliflower-like organization of the dorsal tubercles. However, the presence of an accessory vaginal gland with a spine is not *per se* a diagnostic character of *worki*. Spines in accessory glands are found in quite a few other species, such as *Carminodoris*. The shape of the spine could be a good diagnostic feature, but its infra-specific variation is unknown. The best diagnostic characters for identifying *worki* probably are both the penis and the dorsal color.

Infra-specific character variation.— Besides the above description, which adds some

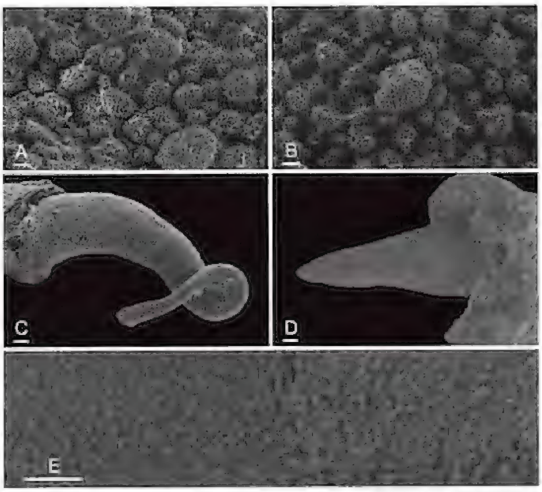

FIGURE 342. *Discodorididae worki*, NMNH 836766. A. Dorsal notum, tubercles, scale = 100 µm.— B. Dorsal notum, tubercles, scale = 100 µm.— C. Penis, scale = 100 µm.— D. Distal accessory gland, spine, scale = 20 µm.— E. Smooth labial cuticle, scale = 20 µm.

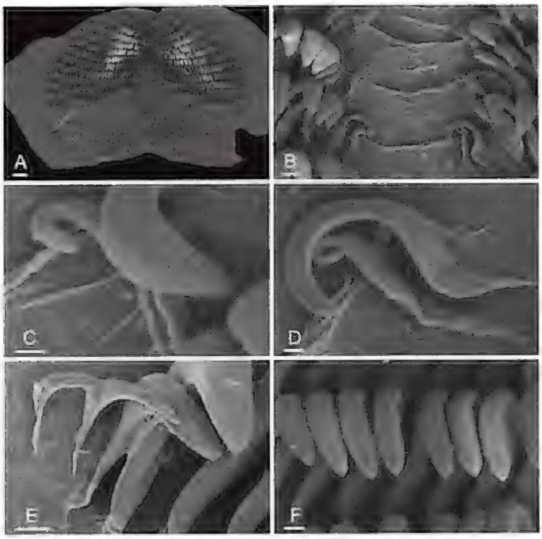

FIGURE 343. *Discodorididae worki*, NMNH 836766. radula. A. Scale = 200 µm.— B. Innermost teeth, scale = 30 µm.— C. Innermost teeth, scale = 10 µm.— D. Innermost teeth, scale = 10 µm.— E. Outermost teeth, scale = 30 µm.— F. Median teeth, scale = 30 µm.

knowledge to the original description, one needs to consider Redfern's (2001) specimen of *worki* was yellow-brown with brown irregular areas.

Discussion.— The additional specimen described here seems to be part of the same unit as the holotype of *worki*. The penial morphology, in particular, is similar. The smaller 'spikelets' described by the Marcus from the type could not be found (even in SEM), but they could have been missed here though. The lack of information regarding the color of the additional specimen (USNM 836766) is regrettable. The specimen identified as *worki* by Redfern (2001) might be part of *worki* because of the presence of the cauliflower-like dorsal tubercles, although the internal anatomy was not described.

Supra-specific relationships.— A phylogenetic test of the relationships of *worki* shows that it is just part of a large metaphyletic group at the base of *Discodorididae*. The Linnaean name should be "*Montereina*" *worki*. Possible names underthe *ICPN* are "*Montereina*" *worki* and *Discodorididae worki*. However, it may just be because few species with an accessory gland with a hollow spine were sampled here. When the diversity of species with accessory glands (with a hollow spine in it) is better understood, then maybe *worki* can be classified more finely.

"*Montereina*" *yaeyamensis* (Baba, 1936) New combination
Discodorididae yaeyamensis (Baba, 1936) New combination

Figures 344-345.

Discodoris yaeyamensis Baba, 1936:30-32, fig. 17, plate 3, fig. 11.

Type material.— Holotype, by monotypy: one specimen 25/12 mm alive, leg. Pr. Oshima, 25 July 1934. Apparently, the holotype was not deposited in a scientific institution. It is probably lost, like most of the types of the species Baba described before World War II (personal communication, Dr. Yoshi Hirano).

Type locality.— Kabira in Ishigaki-shima, [Sakishima Islands, southernmost islands of the Ryukyu Islands, between 24° and 25° S], Japan.

Distribution.— This species is only known from the holotype.

Remarks on the original description (Figs. 344-345).— The original description of *yaeyamensis* is incomplete. However, the color of the live animal is described with precision: "The back is covered with well-marked chocolate mottles on the pale chocolate background; the under surface of the mantle and the foot are yellowish brown with sparsely-set chocolate mottles." Also, Baba's (1936, plate 3, fig. 11) color drawing provides an important character that is not mentioned in the text: white marks on the median line of the dorsal notum. Most other characters described are general and could apply to many other species: e.g., mantle rather soft and wide, dorsal surface covered with 'granules' (i.e., probably tubercles),

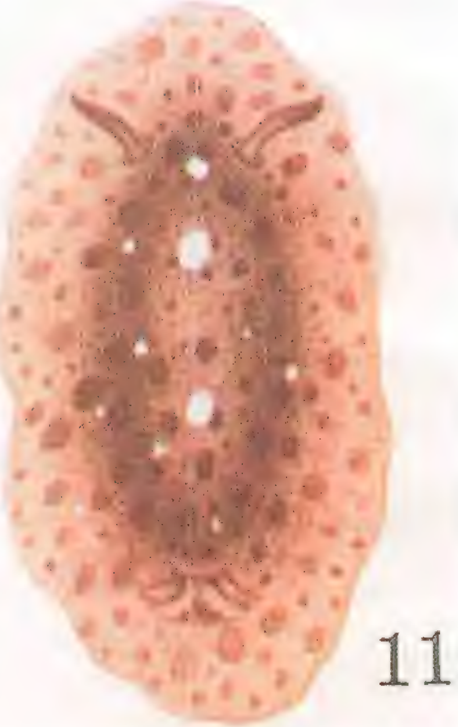

Figure 344. *Discodorididae yaeyamensis*, dorsal color (Baba, 1936: plate 3, fig. 11).

rhinophores retractile in sheaths, six gills retractile in a cavity, foot grooved and "obtusely truncated" at its anterior end, armed labial cuticle, radula with simply hamate teeth, radular formula of 20 × (30-0-30), digitiform oral tentacles. The reproductive system was not described.

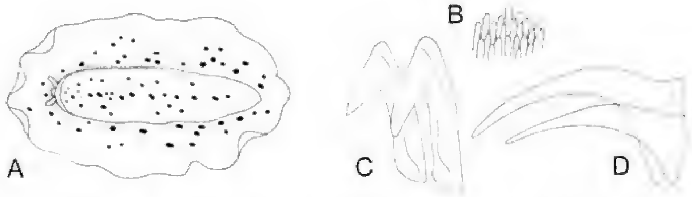

FIGURE 345. *Discodorididae yaeyamensis*, after Baba (1936: fig. 17). A. Ventral view.— B. Jaw rodlets.— C. Lateral teeth.— D. Outermost teeth.

DISCUSSION.— The color of *yaeyamensis* could be regarded as similar to that of *lilacina* (dorsal surface with pale chocolate background, brown spots, and white marks on the median line; hyponotum and foot yellowish with brown dots). Unfortunately, Baba did not describe the reproductive system and the synonymy between *yaeyamensis* and *lilacina* cannot be proposed. Note that *Tayuva lilacina* is known from southern Japan: Robert Bolland collected a specimen of *lilacina* from Okinawa (CASIZ 069969), fully described here. Baba compared *yaeyamensis* with *Halgerda japonica* Eliot, also allocated in *Sclerodoris*, and wrote that both species were much alike in the "form and coloration of the body." This assertion is problematic because it suggests that *yaeyamensis* might have had some dorsal ridges not described by Baba, in which case it could hardly be a synonym of *lilacina*. So, *yaeyamensis* is regarded as a *nomen dubium* for several reasons: 1) the original description is ambiguous; 2) the reproductive system was not described; 3) the type is lost.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *yaeyamensis* shows that it does not belong to *Discodoris*. It is just part of a large metaphyletic group at the base of *Discodorididae*. The Linnaean name should be "*Metadiscodoris*" *yaeyamensis*. Possible names underthe *ICPN* are "*Metadiscodoris*" *yaeyamensis* and *Discodorididae yaeyamensis*.

"*Metadiscodoris*" *ylva* (Marcus, 1965) New combination
Discodorididae ylva (Marcus, 1965) New combination

Figures 346-347.

Discodoris ylva Marcus, 1965:275-276, figs 19-22.

TYPE MATERIAL.— Holotype (NMNH 575377), by original designation, one specimen 11/9 mm preserved, leg. Branner, 1 August 1951.

TYPE LOCALITY.— Onotoa Atoll, Gilbert Islands, [western Pacific].

TYPE MATERIAL CONDITION.— The holotype was entirely dissected by Ernst Marcus. The body wall, the digestive gland, and some pieces of the oral tube remain in the jar. Unfortunately, the reproductive system, the labial cuticle, and the radula, which are not preserved on slides, are probably lost.

DISTRIBUTION.— So far, *ylva* is known from the holotype only.

HABITAT.— On *Heliopora* flat, by tide pooling.

REMARKS ON THE ORIGINAL DESCRIPTION (Figs. 346-347).— Marcus described the dorsal color of the preserved animal as "yellowish, sprinkled with fine black dots on notum, concentrated in many bigger spots." The preserved animal is now white, with a few slightly greyish areas on the dorsal notum, due to a concentration of inconspicuous dark dots. According to Marcus, dorsal tubercles are caryophyllidia. Some caryophyllidia were observed with a dissecting scope, but, strangely enough, they could not be confirmed through SEM because the dorsal notum is in poor condition. Marcus mentioned 14 rhinophoral lamellae, which is probably correct (from 10 to 15 lamellae). The digitiform oral tentacles are not grooved (only the left tentacle remains). The "five or six [outer] transverse folds" described by Marcus on the oral tentacles are hardly distinguishable. The labial cuticle is armed with a pair of jaw rodlets. The radular formula is 21 × (30-0-30). Teeth are simply hamate, except for the two outermost ones that bear from one to five denticles. The reproductive system, especially the connections of the ducts, is unusual, as far as discodorids are concerned. Only one duct opens into the bursa, which results of the fusion of the vaginal duct with the fertilization duct. Two ducts, however, open into the receptaculum seminis: the fertilization duct coming from the bursa, and then another independent duct (called 'short insemination duct' by Marcus) between the receptaculum and the fertilization chamber. Marcus could have confused the receptaculum and the bursa. If his observations are correct, then the genital pattern of *ylva* would be distinct from the pattern typically found in other discodorids. In addition, the original description mentions the presence of a 'soft, pleurembolic penis.'

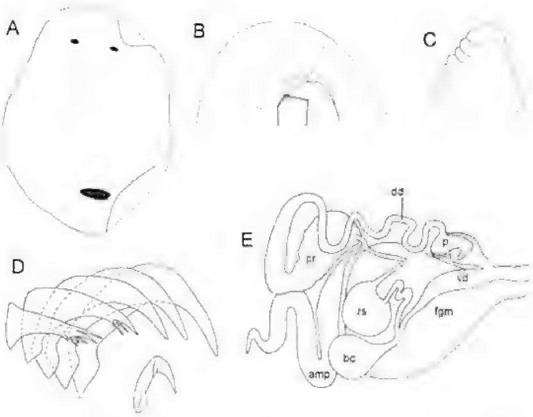

FIGURE 346. *Discodorididae ylva*, holoytype, NMNH 575377. A. Dorsal view, total length = 11 mm.— B. Anterior, ventral view, total width = 7 mm.— C. Oral tentacle, total length = 0.3 mm.— D. Outermost teeth and one innermost tooth, after Marcus (1965: fig. 21).— E. Reproductive system, after Marcus (1965: fig. 22).

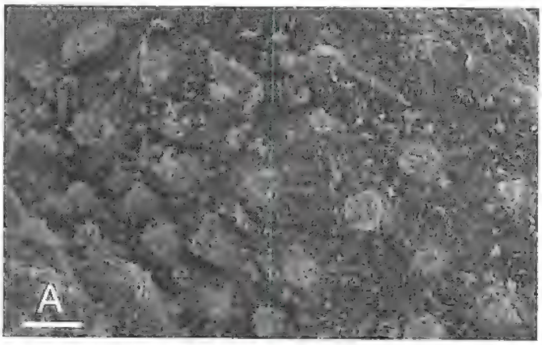

FIGURE 347. *Discodorididae ylva*, holotype, dorsal notum. A. Scale = 100 µm.

DISCUSSION.— It seems that *ylva* belongs to *Discodorididae*, although the reproductive system (if it is as Marcus described it) is unusual. Despite the absence of drawing (or picture) of the dorsal color, this species could probably be re-identified with the dorsal color and the denticulate, outermost teeth. Note, however, that denticles of outermost teeth tend to vary infra-specifically. New specimens from the type locality are needed.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *ylva* shows that it does not belong to *Discodoris*. It is just part of a large metaphyletic group at the base of *Discodorididae*. The Linnaean name should be "*Montereina*" *ylva*. Possible names underthe *ICPN* are "*Montereina*" *ylva* and *Discodorididae ylva*.

"*Montereina*" *zibethina* (Bergh, 1878) New combination
Discodorididae zibethina (Bergh, 1878) New combination

Figure 348.

Fracassa zibethina Bergh, 1878b:598-601, plate LXVI, figs 21-26, plate LXVII, figs 1-2.
Discodoris zibethina.— Valdés, 2002:566, 569, figs 17-18.

TYPE MATERIAL.— Holotype (ZMUC GAS-2112), by monotypy: one specimen 58/26 mm preserved, leg. Semper, March 1865.

TYPE LOCALITY.— [Canal of] Lapinig, Philippines.

TYPE MATERIAL CONDITION.— The holotype was dissected by Bergh, who left the radula and the labial cuticle in the jar. Both the radula and the labial cuticle were mounted on SEM stubs by Valdés, who did not send those stubs back to the ZMUC. Now, only an empty body wall and the branchial plumes remain the jar.

Distribution.— The holotype is the only specimen known.

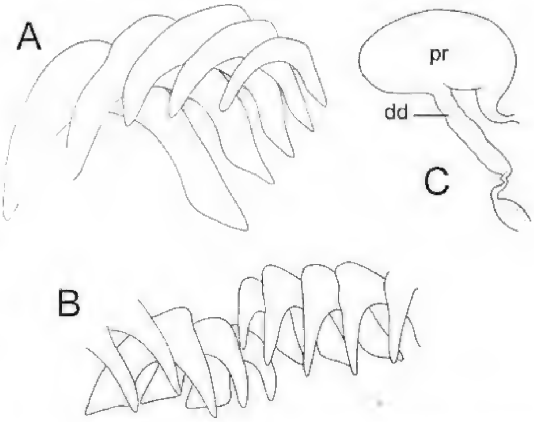

Figure 348. *Discodorididae zibethina*, original illustrations. A. Outermost teeth, after Bergh, (1877a: plate LXVI, fig. 26).— B. Innermost teeth, after Bergh, (1877a: plate LXVI, fig. 23).— C. Prostate and deferent duct, after Bergh (1877a: plate LXVII, fig. 1).

Remarks on the original description (Fig. 348).— The color of the live animal is unknown. Bergh described the dorsal color of the preserved animal as grayish and blackish with blackish blotches. It currently is dirty grayish, colorless. The dorsal notum is covered with small, round tubercles that are not caryophyllidia. The lateral notum is reduced on both sides, maybe because of autotomy. There are six tripinnate branchial plumes, and the margin of the branchial sheath is not lobed. The anterior foot is bilabiate and the upper lip is notched. The two oral tentacles are conical, not grooved. The labial cuticle is armed with jaw rodlets. Bergh described a radular formula of 46 × (82/83-0-82/83), and Valdés (2002), who took SEM pictures of the radula, mentioned a formula of *n* × (83-0-83). Because Valdés did not return the SEM stubs to the ZMUC, this formula cannot be commented on. Bergh described quite a few details of the reproductive system. However, those details are hardly informative without a drawing of the complete reproductive system. However, Bergh illustrated the prostate, the deferent duct, and the penial sheath. The penis is thick, unarmed, and approximately 4.5 mm long. The bursa copulatrix measures 10 mm in diameter, and the receptaculum seminis, sausage-shape, is 8 mm long.

Discussion.— The identification of *zibethina* might remain difficult for quite some time, mainly because of the absence of information on the color of the live animal, and because Bergh did not provide any diagnostic feature in his description. It is unlikely that *zibethina* is another synonym of *Sebadoris fragilis* because of the length of the penis and because of the radular formula (60 mm long *fragilis* specimens tend to have fewer teeth per half row). It clearly belongs to *Discodorididae*. It is unclear whether or not new specimens from the type locality could be re-dentified as *zibethina*. On the one hand, an unarmed 4.5 mm long penis is not commonly found in discodorids, which could be helpful; on the other hand, the absence of data of the exact shape of that penis, and the absence of information on the color of the live animal, will jeopardize any re-identification. Therefore, as rightly proposed by Valdés, *zibethina* should be regarded as a *nomen dubium*.

Supra-specific relationships.— It is hard to understand why Bergh did not place *zibethina* in *Discodoris*, because his diagnosis of *Discodoris* is similar to his diagnosis of *Fracassa*. Maybe, he thought that the nearly nodulose dorsal surface ("*supra subnodulosum*") of *Fracassa* was different from a dorsal surface covered with small granular tubercles ("*supra minute granularum*") of *Discodoris*. The other characters are identical: they are either symplesiomorphies at the level of discodorids (e.g., notched upper lip of the bilabiate anterior foot) or features that are found outside discodorids (e.g., hamate teeth). Valdés (2002) regarded *Fracassa* as a synonym of *Discodoris*. However, this synonymy was not based on a phylogenetic analysis: Valdés did not demonstrate that *zibethina* and *boholiensis* belong to the same clade. A phylogenetic test of the relationships of *zibethina* shows that *zibethina* does not belong to the clade *Discodoris*, but simply is part of a large metaphyletic group at the base of *Discodorididae*. The Linnaean name for *zibethina* should be "*Montereina*" *zibethina*. Possible names under the *ICPN* are "*Montereina*" *zibethina* and *Discodorididae zibethina*.

"*Montereina*" sp. C
Discodorididae sp. C
New, unnamed species

Figures 349-351.

Material dissected.— **Japan**, Honshu, Sagami Bay, Choshaga Saki, 21 June 1970, one specimen 65/55 mm preserved, leg. F. B. Steiner, identified as *Sebadoris nubilosa* by T. M. Gosliner (CASIZ 082038) [the specimen was largely destroyed and poorly preserved externally; the labial cuticle was removed prior to the present study].

Distribution.— Japan, Sagami Bay (~ 35°N, 139°E).

Description (Figs. 349-351).— *Color*. The color of the live animal is unknown. The dorsal notum of the preserved specimen is creamish-brownish, with dark irregular blotches. The hyponotum, the lateral side of the foot, and the pedal sole are covered with many brown dots. The specimen is so poorly preserved that it is even difficult to determine (and describe) its preserved dorsal color. The hyponotum bears a dark ring all around the foot (this ring does not touch the edge of the hyponotum, which is lighter).

External morphology. The body is oval. Its length equals less than twice its width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform, not grooved. The dorsal notum bears conical tubercles that are not caryophyllidia. Some of those tubercles have an apical tail, although it is difficult to determine whether this is natural or just due to preservation. The margin of the gill opening is not star-shaped with five lobes. The branchial plumes could not be counted. There are 35 rhinophoral lamellae.

Digestive system. The stomach is large, free, on top of the left, anterior side of the digestive gland. There is a small caecum. The intestine is straight, dorsal. It is unclear whether the labial cuticle is armed or not. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. The radular formula is: 30 × (60-0-60). The rachidian teeth are absent and the rachidian space is narrow. The rows of lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant, except for the four or six innermost teeth of which the size increases gradually and the last four or six outermost ones of which the size decreases gradually. All teeth are hamate, including the outermost ones. They bear no denticles.

Nervous system. The length of the circum-esophageal nerve ring equals approximately twice the width of the dorsal ganglia. The cerebral, pleural, and pedal ganglia are fused in a general nervous mass covered with small tubercles.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is convoluted (three loops). The division between male and female ducts (in the female gland mass) could not be seen by dissection. The prostate is divided in a proximal part and a distal part. The deferent duct is highly convoluted, with several tight loops. The deferent duct ends in a penis with a distinct morphology. The penis is long (6 mm), narrow, coiled, and bears conical hooks. The latter are arranged in a series of four or five rings in the apical region of the penis. The vaginal duct is loosely convoluted near the genital openings. The fertilization duct is short. The bursa copulatrix is slightly larger than the receptaculum

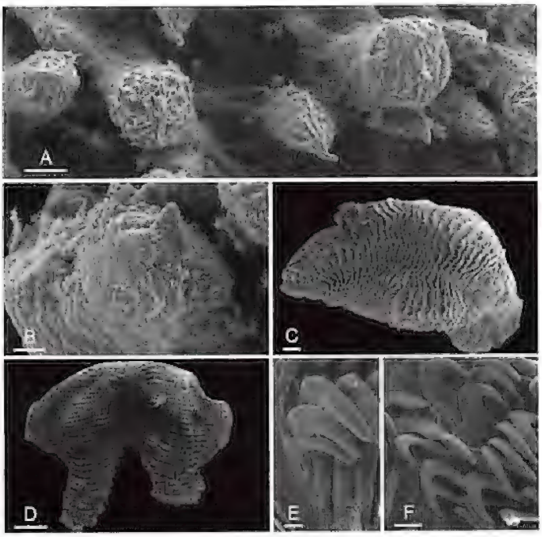

FIGURE 349. *Discodorididae* sp. C, CASIZ 082038. A. Dorsal notum, tubercles, scale = 200 μm.— B. Tubercle, scale = 100 μm.— C. Rhinophore, scale = 200 μm.— D. Radula, scale = 1 mm.— E. Outermost teeth, scale = 20 μm.— F. Innermost teeth, scale = 60 μm.

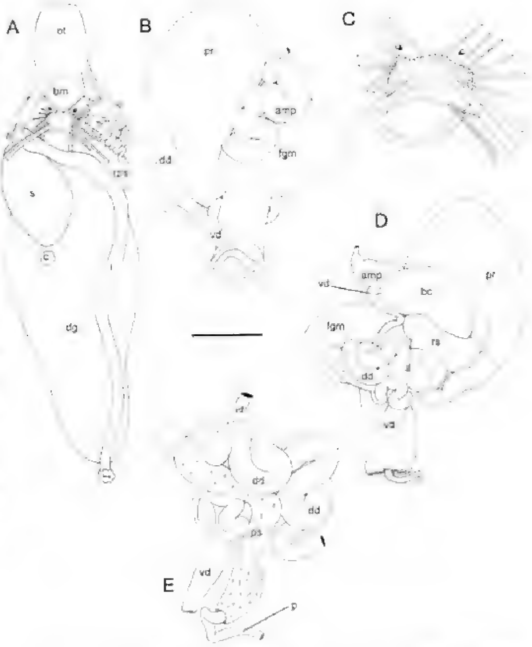

FIGURE 350. *Discodorididae* sp. C, CASIZ 082038. A. General anatomy, scale = 7 mm.— B. Reproductive system, scale = 3 mm.— C. Nervous system, scale = 2 mm.— D. Reproductive system, Scale = 3 mm.— D. Distal part of the reproductive system, detail, scale = 2.4 mm.

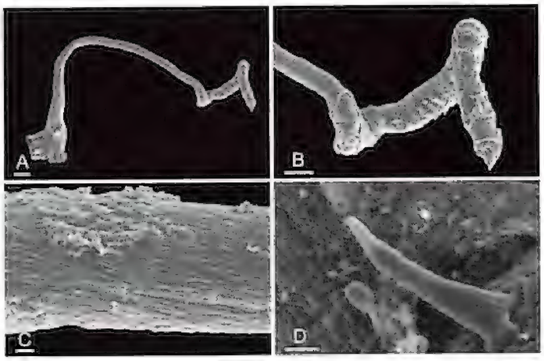

FIGURE 351. *Discodorididae* sp. C, penis, CASIZ 082038. A. Scale = 300μm.— B. Scale = 200 μm.— C. Scale = 40 μm.— D. Scale = 10 μm.

seminis. Both pouches are spherical-ovate and smooth.

DISCUSSION.— This specimen has a peculiar penis, which clearly is diagnostic of a species. It can hardly be mistaken with any other copulatory organs. Baba (1949, 1955) studied the molluscan fauna from Sagami Bay. Nearby localities have been explored as well, such as the Izu Islands by Suzuki (2000). Therefore, it cannot be excluded that this new species has been misidentified in the past. However, without information on the reproductive system, it is not possible to determine whether or not this species has been misidentified. The fact that the specimen dissected was misidentified as *Sebadoris nubilosa* indicates that this species may continue being overlooked unless people dissect the reproductive system. Of course, one of the main difficulties is that we know nothing about the color of the live animal dissected here. In cases where identifications are not certain, people should always take a picture *and* deposit the specimen photographed in a museum collection for future anatomical study. In any case, discovering what this new species actually looks like will require future workers to take pictures of brownish specimens (with a dark ring on the hyponotum) and then dissect the reproductive system to check whether or not they have a penis similar to the penis described here. Although the penis is clearly distinct, this new species is not named: the color of live animals is unknown, and nothing is known about the infra-specific variation of the anatomy, especially the diagnostic penial morphology.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of sp. C shows that it is part of a large metaphyletic group at the base of *Discodorididae*. Sp. C should be referred to as "*Metadiscodoris*" sp. C or *Discodorididae* sp. C (*ICPN*).

"*Montereina*" sp. D
Discodorididae sp. D
New, unnamed species

Figures 352-358.

MATERIAL DISSECTED.— **[Eastern Pacific Ocean]**, Ecuador, Galapagos Islands, Isla Isabela, Punta Vicente Roca, 23 meters depth, 15 May 1994, four specimens 13/7 (#1), 13/7 (#2), 8/5 (#3), and 4/2 (#4) mm preserved, leg. T. M. Gosliner aboard "Mistral II," identified as *Tayuva ketos* by T. M. Gosliner and Y. Camacho-García (CASIZ 097534) [one of the two largest specimens were dissected by Yolanda Camacho-García and Terrence M. Gosliner]; Ecuador, Galapagos Islands, Isla Isabela, Punta Vicente Roca, 35 meters maximum depth, 14 May 1994, six specimens 14/7 (#1), 12/6 (#2), 11/5 (#3), 10/5 (#4), 10/5 (#5), and 9/5 (#6) mm preserved, leg. T. M. Gosliner aboard "Mistral II," identified as *Tayuva ketos* by T. M. Gosliner and Y. Camacho-García (CASIZ 097574).

DISTRIBUTION. —Galapagos Islands.

DESCRIPTION (Figs. 352-358).— *Color*. The live dorsal color of the specimens dissected here is unknown. Since they were misidentified as *Tayuva ketos*, they probably had a dorsal creamish background with brown spots. All preserved specimens are homogeneously whitish or creamish.

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform but not grooved. Caryophyllidia are present. Many small holes (diameter < 10 μm) and small tufts of cilia are present on the surface of the mantle, including the tubercles, the gills, and the rhinophores. In preserved specimens, the margins of the branchial and rhinophoral sheaths can be smooth or lightly crenulate. There are six tripinnate branchial plumes arranged in circle around the anus. The rhinophores have up to 15 lamellae.

Digestive system. The stomach is free, on top of the left side of the digestive gland. A small caecum is located on the left, posterior side of the stomach. The intestine is straight and dorsal. The labial cuticle is armed with two sickle-shaped jaw plates that consist of rodlets. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. Radular formulae are: 11 × (31-0-31) in a 14 mm long specimen (CASIZ 097574 #1), 16 × (21-0-21) in a 10 mm long specimen (CASIZ 097574 #4), 11 × (22-0-22) in a 10 mm long specimen (CASIZ 097574 #5), 19 × (25-0-25) in a 13 mm long specimen (CASIZ 097534 #2), 16 × (22-0-22) in a 8 mm long specimen (CASIZ 097534 #3), and 12 × (13-0-13) in a 4 mm long specimen (CASIZ 097534 #4). Rachidian teeth are absent. The rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis. The tooth size increases gradually towards the middle of a half row, then remains more or less stable, and then decreases towards the outermost teeth. The two last outermost teeth, which may not be hamate, bears a few denticles (from one to five).

Nervous system. The length of the circum-esophageal nerve ring equals less than twice the width of the cerebro-pleural ganglia. The ganglia are fused, but can still be distinguished on the (smooth) surface.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is convoluted. The division between male and female ducts, embedded within the female gland mass, could not be seen by dissection. The prostate is divided in a proximal part and a distal part. The deferent duct is convoluted and presents a distinct organization, i.e., two loops on the surface of the bursa copulatrix. Those two dis-

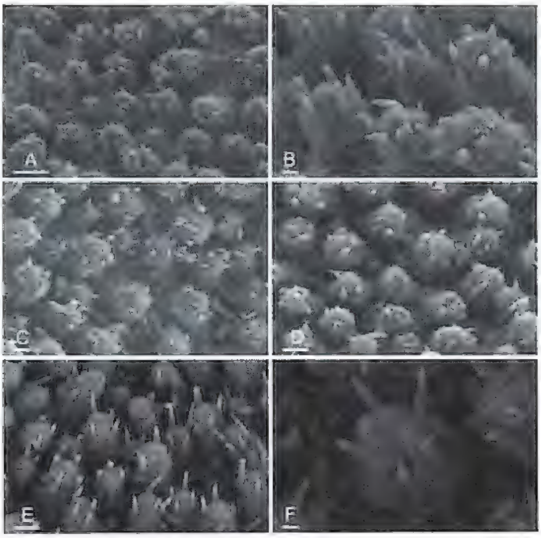

FIGURE 352. *Discodorididae* sp. D, dorsal notum, tubercles. A. CASIZ 097574 (#1), scale = 100 µm.— B. CASIZ 097574 (#1), scale = 20 µm.— C. CASIZ 097574 (#2), scale = 30 µm.— D. CASIZ 097534 (#2), scale = 20 µm.— E. CASIZ 097534 (#3), scale = 20 µm.— F. CASIZ 097534 (#3), scale = 10 µm.

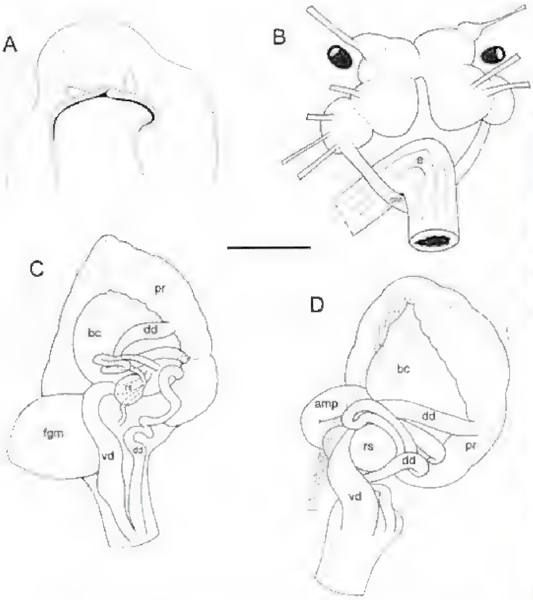

FIGURE 354. *Discodorididae* sp. D. A. Anterior, ventral view, CASIZ 097574 (#4), total width = 10 mm.— B. Nervous system, CASIZ 097574 (#4), scale = 0.5 mm.— C. Reproductive system, CASIZ 097574 (#4), scale = 1 mm.— D. Reproductive system, CASIZ 097534 (#3), scale = 0.5 mm.

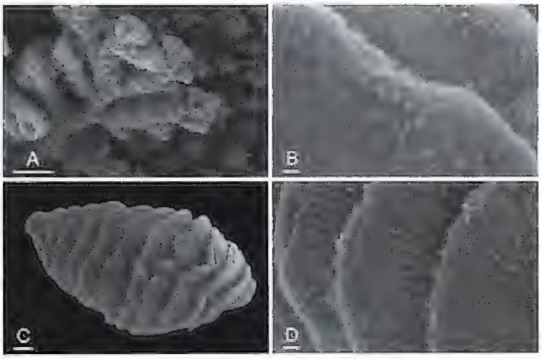

FIGURE 353. *Discodorididae* sp. D, rhinophores and gills. A. Branchial plume, CASIZ 097534 (#3), scale = 100µm.— B. Rhinophoral lamellae, CASIZ 097574 (#3), scale = 10µm.— C. Rhinophore, CASIZ 097574 (#5), scale = 100µm.— D. Rhinophoral lamellae, CASIZ 097574 (#5), scale = 20µm.

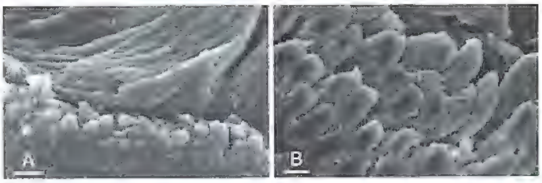

FIGURE 355. *Discodorididae* sp. D, jaw rodlets. A. CASIZ 097534 (#3), scale = 10 µm.— B. CASIZ 097574 (#4), scale = 5 µm.

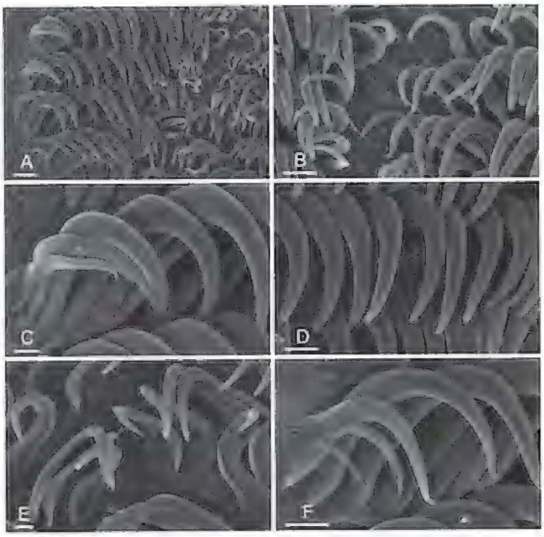

FIGURE 356. *Discodorididae* sp. D, radula. A. Left rows, CASIZ 097574 (#5), scale = 30 µm.— B. Innermost teeth, CASIZ 097574 (#5), scale = 20 µm.— C. Outermost teeth, CASIZ 097574 (#5), scale = 10 µm.— D. Median teeth, CASIZ 097574 (#1), scale = 20 µm.— E. Innermost teeth, CASIZ 097574 (#1), scale = 10 µm.— F. Outermost teeth, CASIZ 097574 (#1), scale = 20 µm.

tinct loops were found in all specimens. The copulatory organ is a small (up to 0.4 mm long), unarmed, conical penis. The vaginal duct is straight. The fertilization duct is straight and short. The connection between the fertilization duct and the female gland mass is marked by a short duct. Both the connection of the receptaculum seminis duct to the receptaculum seminis and the disappearance of the fertilization duct into the female gland mass (where it connects to the fertilization chamber) are underneath the receptaculum seminis. The bursa copulatrix is much larger than the receptaculum seminis. Both spermatic pouches are spherical-ovate, close to each other.

Discussion.— Those specimens are close to *Discodorididae mortenseni*, from the Caribbean Sea. In fact, specimens of *mortenseni* cannot be distinguished from those Galapagos specimens. The denticles of the outermost teeth tend to be longer in the radula of the Caribbean specimens, but those denticles vary a great deal and it is not possible to determine whether or not those differences have a real taxonomic meaning (they likely do not). However, Galapagos specimens probably are part of a distinct species, because of geographical isolation, they are referred here as sp. D. In the future, we will need additional data to test whether or not *mortenseni*-like specimens from Caribbean and Galapagos are part of a single species or are two closely related species. Also, the color of live animals from the Galapagos is still not documented, and the color of live animals from the Caribbean Sea is still poorly known.

Supra-specific relationships.— A phylogenetic test of the relationships of sp. D shows that it is part of a large metaphyletic group at the base of *Discodorididae*. Sp. D should be referred to as "*Montereina*" sp. D, under the ICZN, or "*Metadiscodoris*" sp. D and *Discodorididae* sp. D, under the *ICPN*.

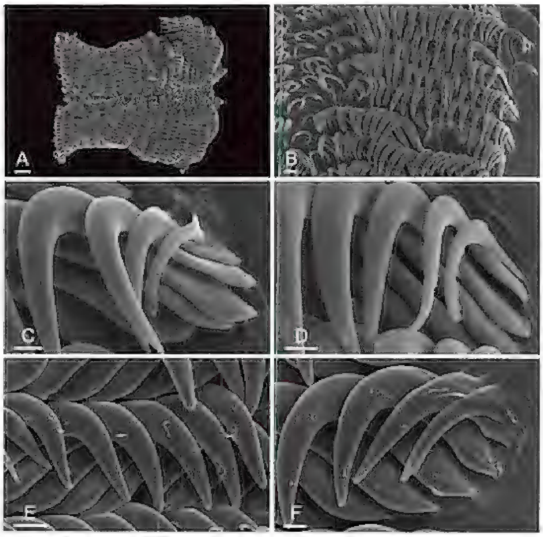

FIGURE 357. *Discodorididae* sp. D, radula. A. Radula, CASIZ 097534 (#2), scale = 100 μm.— B. Right rows, CASIZ 097534 (#2), scale = 30 μm.— C. Outermost teeth, CASIZ 097534 (#2), scale = 10 μm.— D. Outermost teeth, CASIZ 097534 (#3), scale = 10 μm.— E. Median teeth, CASIZ 097574 (#4), scale = 20 μm.— F. Outermost teeth, CASIZ 097574 (#4), scale = 10 μm.

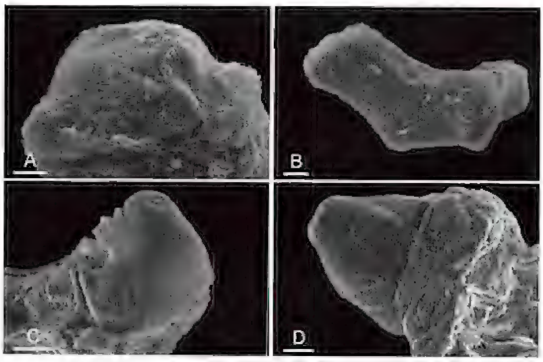

FIGURE 358. *Discodorididae* sp. D, penis. A. CASIZ 097574 (#1), scale = 30 μm.— B. CASIZ 097574 (#3), scale = 30 μm.— C. CASIZ 097574 (#5), scale = 100 μm.— D. CASIZ 097574 (#6), scale = 100 μm.

"*Montereina*" sp. E
Discodorididae sp. E
New, unnamed species

Figures 359-367.

Material dissected.— **Mexico**, Baja California Sur, Gulf of California, Isla Coronados Point, 20 meters depth, 30 June 1987, three specimens 17/10 (#1), 13/8 (#2), and 9/6 (#3) mm preserved, leg. T. M.

Gosliner and H. Bertsch, identified as *Discodorididae* by T. M. Gosliner (CASIZ 071657) [these specimens are poorly preserved]; Mexico, Baja California Sur, Gulf of California, Isla Coronados Point, 20 meters depth, 30 June 1987, two specimens 16/7 (#1) and 10/5 (#2) mm preserved, leg. T. M. Gosliner, identified as *Discodorididae* by T. M. Gosliner (CASIZ 071810); Mexico, Baja California, Gulf of California, Bahia de Los Angeles, Punta Gringa, northeast side, 4 meters depth, 2 October 1984, one specimen 7/4 mm preserved, leg. T. M. Gosliner, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 072928); Mexico, Baja California, Gulf of California, Bahia de Los Angeles, Punta Gringa, northeast side, 4 meters depth, 3 October 1984, one specimen 10/5 mm preserved, leg. H. Bertsch, identified as *Discodoris fragilis* by T. M. Gosliner (CASIZ 072932); Mexico, Baja California, Gulf of California, Bahia de Los Angeles, Punta Gringa, 10 meters depth, 30 June 1987, one specimen 14/10 mm preserved, leg. H. Bertsch, identified as *Discodoris* by T. M. Gosliner (CASIZ 071871).

Distribution. —Gulf of California.

Habitat.— Off rock (CASIZ 072932, CASIZ 072928).

Description (Figs. 359-367).— *Color.* The live dorsal color of the specimens dissected here is unknown. Since some of them were misidentified as *Discodoris fragilis*, they probably had a dorsal creamish-grey background with brown spots. Preserved specimens have a creamish dorsal background with traces of spots (CASIZ 071657, 071810, 071871) or entirely white (CASIZ 072932).

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform but not grooved. Tubercles are caryophyllidia. Many small holes (diameter < 10 µm) and small tufts of cilia are present on the surface of the mantle, including the tubercles, the gills, and the rhinophores. In preserved specimens, the margins of the branchial and rhinophoral sheaths can be smooth or lightly crenulate. There are six tripinnate branchial plumes arranged in circle around the anus. The rhinophores have up to 12 lamellae.

Digestive system. The stomach is free, on top of the left side of the digestive gland. A small caecum is located on the left, posterior side of the stomach. The intestine is straight and dorsal. The labial cuticle is smooth, except in one individual (CASIZ 071871) where it is armed with two or three rudimentary rows of rodlets. The length of the radula approximately equals twice its width. The radular sac cannot be seen by dorsal dissection. Radular formulae are: 15 × (20-0-20) in a 14 mm long specimen (CASIZ 071871), 14 × (18-0-18) in a 7 mm long specimen (CASIZ 072928), 15 × (27-0-27) in a 9 mm long specimen (CASIZ 071657 #3), 15 × (27-0-27) in a 17 mm long specimen (CASIZ 071657 #1), 14 × (18-0-18) in a 10 mm long specimen (CASIZ 072932), and 16 × (21-0-21) in a 16 mm long specimen (CASIZ 071810 #1). The radular formula could not be determined for one individual (CASIZ 071810 #2). Rachidian teeth are absent. The rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis. The tooth size increases gradually towards the middle of a half row, then remains more or less stable, and then decreases towards the outermost teeth. The few last outermost teeth sometimes bear a few denticles (from one to five). The number of denticulate teeth ranges from zero to three, and the number of denticles per tooth ranges from zero to five. However, these numbers vary among individuals, and even among rows of a single radula.

Nervous system. The length of the circum-esophageal nerve ring equals less than twice the width of the cerebro-pleural ganglia. The ganglia are fused. Their surface is smooth.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is convoluted. The division between male and female ducts, within the female gland mass, could not be seen by dissection. The prostate is divided in a proximal part and a distal part. The vaginal, fertilization, and deferent duct are arranged in a distinct organization that can hardly be described with words: the deferent duct runs

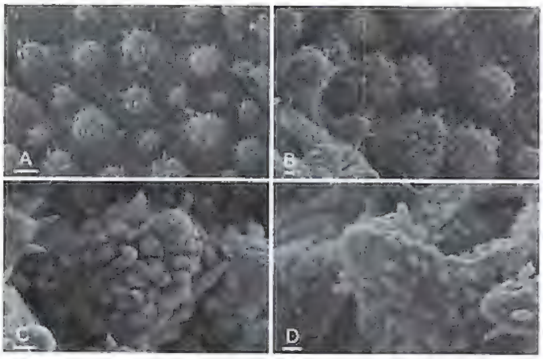

Figure 359. *Discodorididae* sp. E, dorsal notum, tubercles. A. CASIZ 071871, scale = 100μm.— B. CASIZ 072932, scale = 20μm.— C. CASIZ 072932, scale = 20μm.— D. CASIZ 072932, scale = 20μm.

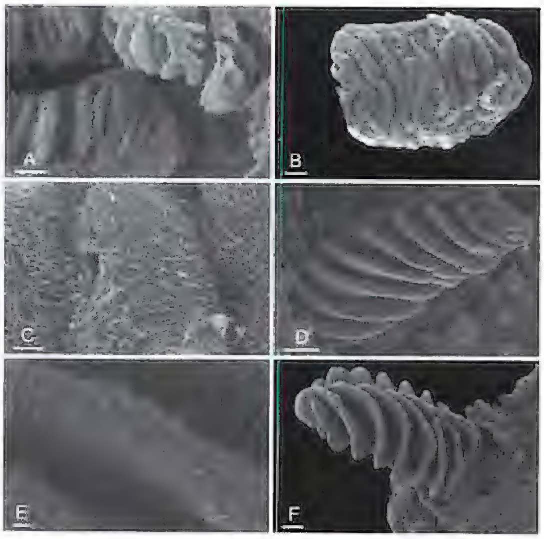

Figure 360. *Discodorididae* sp. E, rhinophores and gills. A. Branchial plumes, CASIZ 071871, scale = 100 μm.— B. Rhinophore, CASIZ 071871, scale = 100 μm.— C. Rhinophoral lamellae, CASIZ 071871, scale = 20 μm.— D. Rhinophore, CASIZ 072928, scale = 100 μm.— E. Rhinophoral lamellae, CASIZ 072928, scale = 10 μm.— F. Rhinophore, CASIZ 072932, scale = 100 μm.

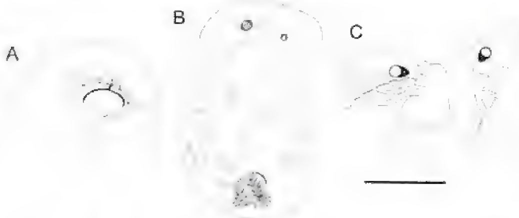

Figure 361. *Discodorididae* sp. E. A. Anterior, ventral view, CASIZ 072829, total width = 4 mm.— B. Rhinophore, CASIZ 071810 (#1), total width = 7 mm.— C. Nervous system, CASIZ 071810 (#1), scale = 1 mm.

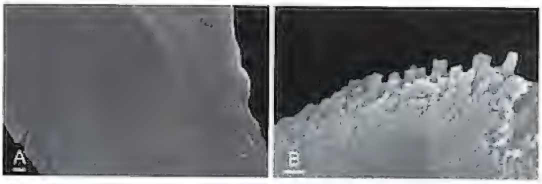

Figure 362. *Discodorididae* sp. E, labial cuticle. A. Smooth labial cuticle, CASIZ 071810 (#1), scale = 20 μm.— B. Jaw rodlets, CASIZ 071871, scale = 10 μm.

on top of the bursa copulatrix, then is convoluted with two or three loops; the fertilization duct is convoluted with three tight loops located near the loops of the deferent duct. The vaginal duct is straight. Both the vagina and the distal end of the deferent duct are enlarged, but with nothing internally (no penis, no spines orhooks). The loops of the deferent and fertilization ducts separate the receptaculum seminis from the bursa copulatrix. The bursa is much larger than the receptaculum. The bursa is partly covered with the prostate. Both pouches are smooth. Both are ovate, although the receptaculum tends to be slightly elongate. The deferent duct ends with an unarmed papilla, which is not a distinct penis. The connection between the fertilization duct and the female gland mass is marked by a short duct.

Discussion.— A peculiar organization of the reproductive system suggest that all those specimens can be grouped together. Also, they share a similar radula, acknowledging that the presence of denticles on outermost teeth varies among and within individuals. The presence of a rudimentary armed labial cuticle in one individual suggests that this individual might not be part of a different unit. However, its reproductive system is hardly distinguishable from that of other specimens, which is why it is not described separately. Also, its rodlets would have probably been missed without SEM, and this new species might be similar to *Discodorididae aurila* in which labial cuticle can, exceptionally, bear some rodlets. However, further investigation is clearly needed to test whether or not all those specimens are part of a single entity.

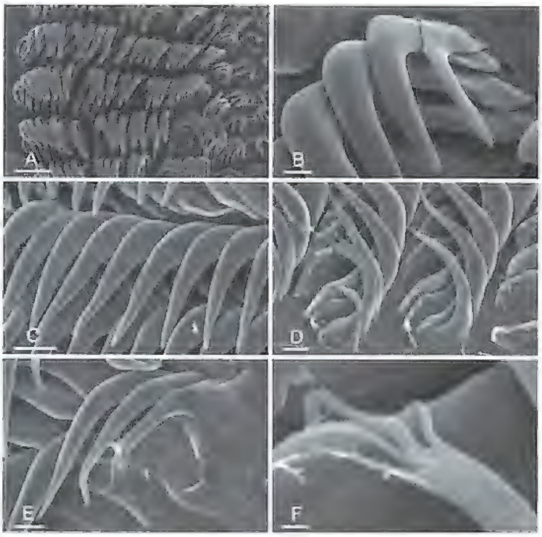

FIGURE 363. Sp. E, radula. A. Left rows, CASIZ 071657 (#3), scale = 100 µm.— B. Outermost teeth, CASIZ 071657 (#3), scale = 20 µm.— C. Median teeth, CASIZ 072932, scale = 20 µm.— D. Outermost teeth, CASIZ 072932, scale = 10 µm.— E. Outermost teeth, CASIZ 072932, scale = 10 µm.— F. Outermost teeth, apical denticles, CASIZ 072932, scale = 2µm.

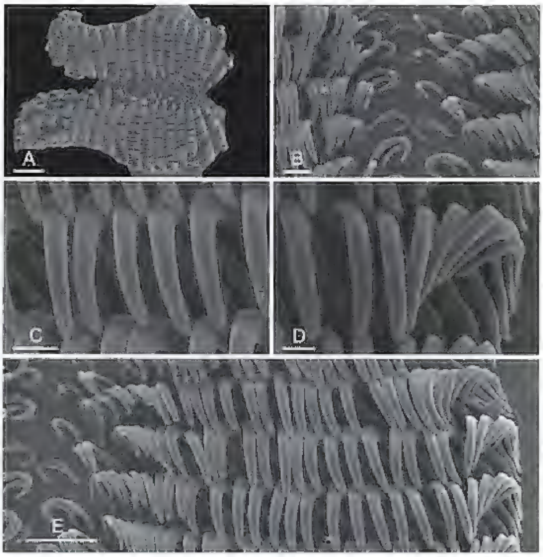

FIGURE 364. *Discodorididae* sp. E, radula, CASIZ 071657 (#1). A. Radula, scale = 200 µm.— B. Innermost teeth, scale = 40 µm.— C. Median teeth, scale = 30 µm.— D. Outermost teeth, scale = 20 µm.— E. Right rows, scale = 100µm.

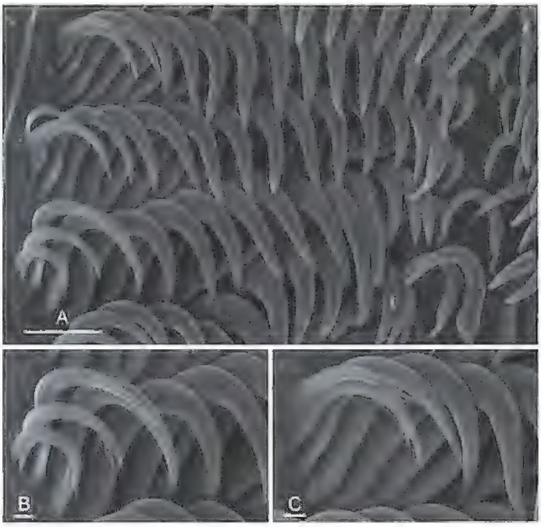

FIGURE 365. *Discodorididae* sp. E, radula, CASIZ 072928. A. Left rows, scale = 100 µm.— B. Outermost teeth, scale = 20 µm.— C. Outermost teeth, scale = 20 µm.

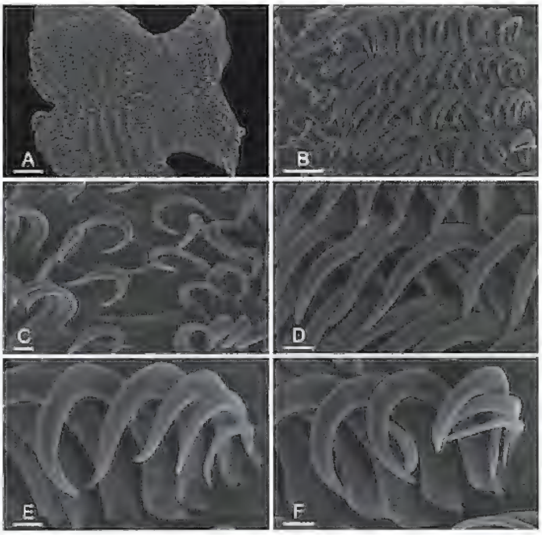

FIGURE 366. *Discodorididae* sp. E, radula, CASIZ 071871. A. Radula, scale = 200 µm.— B. Right rows, scale = 100 µm.— C. Innermost teeth, scale = 20 µm.— D. Median teeth, scale = 20 µm.— E. Outermost teeth, scale = 20 µm.— F. Outermost teeth, scale = 20 µm.

One of the main issues faced here was that the color of live animals was unknown. They probably are *Tayuva lilacina*-like, i.e., creamish dorsal background with brown spots, but we obviously need to know their actual color alive before creating a new species name. Several species (both from eastern Pacific and the Caribbean) have outermost teeth with similar denticles, such as *Discodorididae mortenseni* and *Discodorididae aurila*. However, they have a different reproductive system: the differences in how the ducts (fertilization, vaginal, deferent) are organized are subtle but real.

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of sp. E shows that it is part of a large metaphyletic group at the base of *Discodorididae*. Sp. E should be referred to as "*Montereina*" sp. E, under the ICZN, or "*Montereina*" sp. E and *Discodorididae* sp. E, under the *ICPN*.

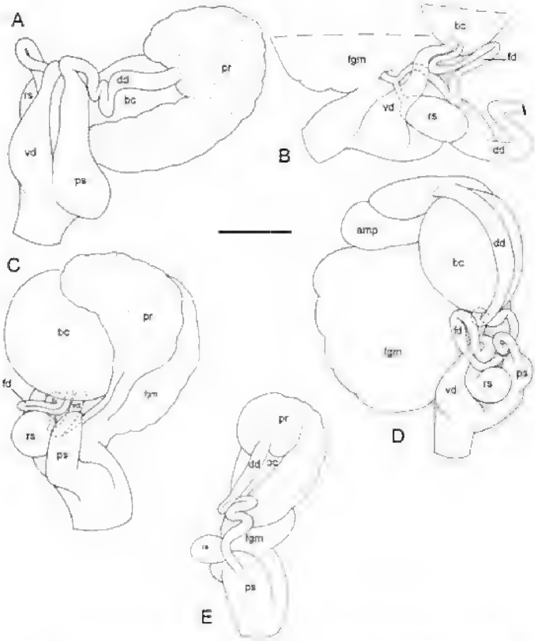

FIGURE 367. *Discodorididae* sp. E, reproductive system. A. CASIZ 072932, scale = 0.6 mm.— B. Spermatic pouches and ducts, CASIZ 071810 (#1), scale = 0.8 mm.— C. CASIZ 071657 (#2), scale = 1 mm.— D. Spermatic pouches and ducts, CASIZ 071810 (#1), scale = 1 mm.— E. CASIZ 072928, scale = 0.5 mm.

"*Montereina*" sp. F
Discodorididae sp. F
New, unnamed species

Figures 368-370.

MATERIAL DISSECTED.— **Philippines,** Luzon, Batangas Province, Calumpan Peninsula, Arthur's Rock, 7 May 2001, one specimen 30/15 mm preserved, leg. T. M. Gosliner, identified as *Discodoris* by T. M. Gosliner (CASIZ 156663).

DISTRIBUTION.— Philippines.

DESCRIPTION (Figs. 368-370).— *Color*. The dorsal notum of the live animal is light brown, mottled with darker spots ofvarious sizes. Most tubercles have a color similar to the background, except for a few tubercles that are white, some of which are arranged along a median line between the rhinophores and the gills. The preserved specimen has a creamish dorsal background, with traces of spots.

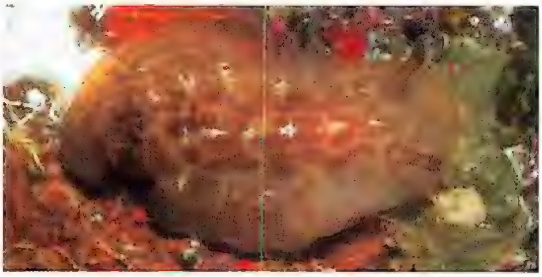

FIGURE 368. *Discodorididae* sp. F, dorsal color (T.M. Gosliner), CASIZ 156663, total length = 30 mm (preserved).

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform but not grooved. Tubercles are caryophyllidia. Many small holes (diameter < 10 μm) and small tufts of cilia are present on the surface of the mantle, including the tubercles, the gills, and the rhinophores. There are six tripinnate branchial plumes arranged in circle around the anus. There are 18 rhinophoral lamellae.

Digestive system. The stomach is free, on top of the left side of the digestive gland. The latter was small, but this is certainly artificial. A small caecum is located on the left, posterior side of the stomach. The intestine is straight and dorsal. The labial cuticle is smooth. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. The radular formula is 19 × (30-0-30). Rachidian teeth are absent. The rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis. The tooth size increases gradually up to the tenth lateral tooth, then remains more or less constant, and then decreases for the last four or five outermost teeth. The teeth bear no denticles and are not grooved.

Nervous system. The length of the circum-esophageal nerve ring equals three times the width of the dorsal (fused and smooth) ganglia.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is convoluted. The division between male and female ducts, within the female gland mass, could not be seen by dissection. The prostate is divided in a proximal part and a distal part. The deferent duct is convoluted with several loops. It seems to be lightly folded internally in its proximal part. It ends in a penial sheath protecting a large, unarmed penis. The vaginal duct is straight. The fertilization duct is straight as well, but long. The duct of the receptaculum seminis is also long (compared to what was usually observed). The deferent duct follows one side of the elongate receptaculum seminis, which gives the reproductive system a peculiar organization. The ovate bursa copulatrix is much larger than the receptaculum. Both pouches are smooth. The penial sheath and the vaginal duct enter a vestibule that might be surrounded by a muscular wall (see, *Tayuva*). However, if this muscular wall is present here, it is thin and inconspicuous. The presence of a muscular wall in this species cannot be regarded as certain.

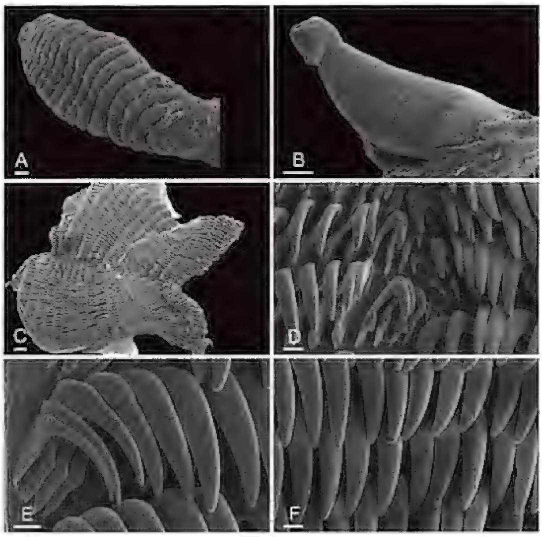

FIGURE 369. *Discodorididae* sp. F, CASIZ 156663. A. Rhinophore, scale = 100 µm.— B. Penis, scale = 100 µm.— C. Radula, scale = 100 µm.— D. Innermost teeth, scale = 20 µm.— E. Outermost teeth, scale = 20 µm.— F. Median teeth, scale = 20 µm.

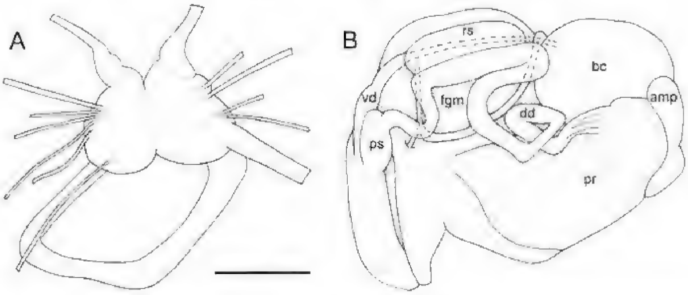

FIGURE 370. *Discodorididae* sp. F, CASIZ 156663. A. Nervous system, scale = 0.8 mm.— B. Reproductive system, scale = 1.5 mm.

DISCUSSION.— This specimen is part of a new, unnamed species. It may be confused with *Tayuva lilacina*, although its dorsal color is darker than *lilacina*. However, lighter variants, which likely exist, probably have been (and will be) overlooked. If fact, we cannot exclude that this species has already been found and misidentified by some workers as *Discodoris concinna*, *Discodoris concinniformis*, or *Discodoris fragilis*. However, the literature rarely provides any information on the genital anatomy, so we will never be able to check whether or not this new species was already found. In any case, no valid name seems to exist for it in the existing literature.

Obviously, further data are needed before we can name this new species. In particular, we need to address the infra-specific variation of several critical features, such as the penial morphology and the color. Its penis will be a good diagnostic character once we better know how it varies among individuals. The presence of a muscular wall in the distal part of the reproductive system is largely hypothetical. If this were to be confirmed, then this species would likely be part of *Tayuva*.

Supra-specific relationships.— A phylogenetic test of the relationships of sp. F shows that it is part of a large metaphyletic group at the base of *Discodorididae*. Sp. F should be referred to as "*Montereina*" sp. F, under the ICZN, or "*Montereina*" sp. F and *Discodorididae* sp. F, under the *ICPN*.

"*Montereina*" sp. G
Discodorididae sp. G
New, unnamed species

Figures 371-374.

Material dissected.— **Fiji** Islands, Viti Levu, Suva Bay, Mosquito Island, 18°07'S, 178°24'E, 13 March 1976, one specimen 25/20 mm preserved, leg. Antonio J. Ferreira, identified as *Sebadoris nubilosa* by Terry Gosliner (CASIZ 082027).

Distribution.— Fiji.

Description (Figs. 371-374).— *Color*. The color of the live animal is unknown. Based on its preserved color (creamish with darker spots), it probably looked like *Sebadoris fragilis* or *Tayuva lilacina*, i.e., light brown background with darker blotches and spots. Two longitudinal rows of large dark blotches can be observed on either side of the median line. The ventral surface of the preserved specimen is creamish with dark spots and dots.

External morphology. The body is oval. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate and the upper lip is notched. The two oral tentacles are digitiform but not grooved. Tubercles are not caryophyllidia. Many small holes (diameter < 10 µm) and small tufts of cilia are present on the surface of the mantle, including the tubercles, the gills, and the rhinophores. There are six tripinnate branchial plumes arranged in circle around the anus. There are 30 rhinophoral lamellae.

Digestive system. The stomach is free, on top of the left side of the digestive gland. A small caecum is located on the left, posterior side of the stomach. The intestine is straight and dorsal. The labial cuticle is armed with a pair of jaws. The length of the radula equals less than twice its width. The radular sac cannot be seen by dorsal dissection. The radular formula is 21 × (41-0-41). Rachidian teeth are absent. The rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis. The tooth size increases gradually up to the tenth lateral tooth, then remains more or less constant, and then decreases for the last five or six outermost teeth. The teeth bear no denticles and are not grooved.

Nervous system. The length of the circum-esophageal nerve ring equals twice the width of the dorsal ganglia.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is convoluted. The division between male and female ducts, within the female gland mass, could not be seen by dissection. The prostate is divided in a proximal part and a distal part. The deferent duct is almost straight. It ends in a long, cylindrical penial sheath protecting a long, cylindrical, armed penis. The latter is 1.2 mm long. It bears strong hooks on one side, from its base up to almost its apex. Most of the hooks are bifid and measure up to 30 µm in length. The apex of the penis looks like as if it was covered with a cap. The arrangement of the fertilization and vaginal ducts could not be established clearly. Both ducts are large (which is unusual for the fertilization duct). It is unclear where the fertilization duct enters the female gland mass. Also, both the fertilization and vaginal ducts are straight. The spherical-ovate bursa copulatrix is much larger than the ovate-elongate receptaculum seminis. Both pouches are smooth.

Discussion.— At first, externally, this specimen was interpreted as a young *Sebadoris frag-*

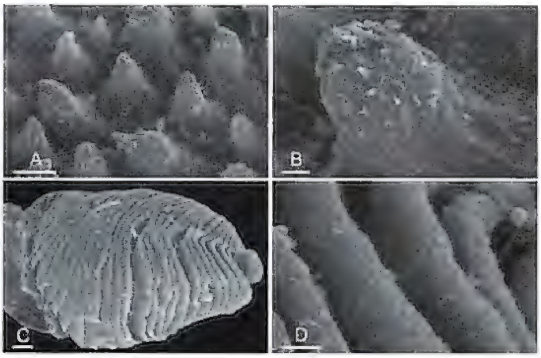

FIGURE 371. *Discodorididae* sp. G, dorsal notum, CASIZ 082027. A. Dorsal notum, tubercles, scale = 200 µm.— B. Dorsal notum, tubercle, scale = 40 µm.— C. Rhinophore, scale = 100 µm.— D. Rhinophoral lamellae, scale = 20 µm.

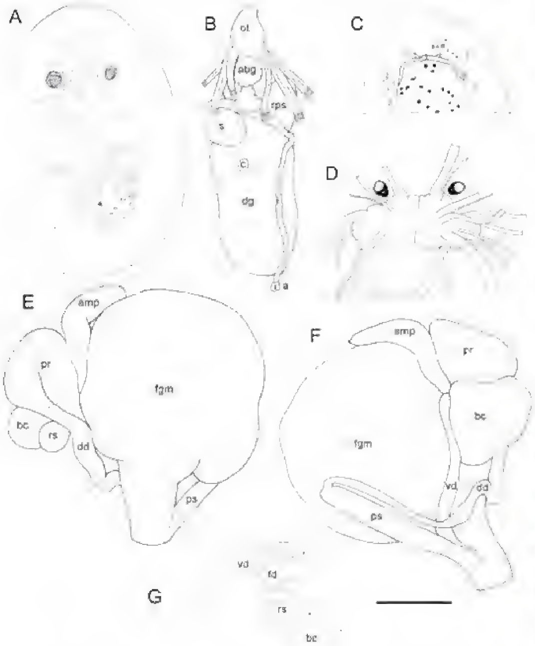

FIGURE 372. *Discodorididae* sp. G, CASIZ 082027. A. Dorsal view, as currently preserved, total width = 20 mm.— B. General anatomy, scale = 3.3 mm.— C. Anterior, ventral view, total width = 20 mm.— D. Nervous system, scale = 1 mm.— E. Reproductive system, scale = 1.2 mm.— F. Reproductive system, scale = 1.2 mm.— G. Spermatic pouches and ducts, scale = 1.2 mm.

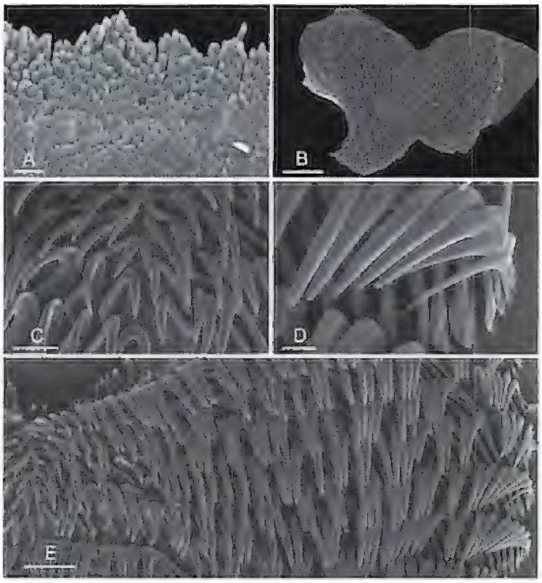

FIGURE 373. *Discodorididae* sp. G, radula and jaws, CASIZ 082027. A. Jaw rodlets, scale = 20 µm.— B. Radula, scale = 400 µm.— C. Innermost teeth, scale = 40 µm.— D. Outermost teeth, scale = 20 µm.— E. Right rows, scale = 100 µm.

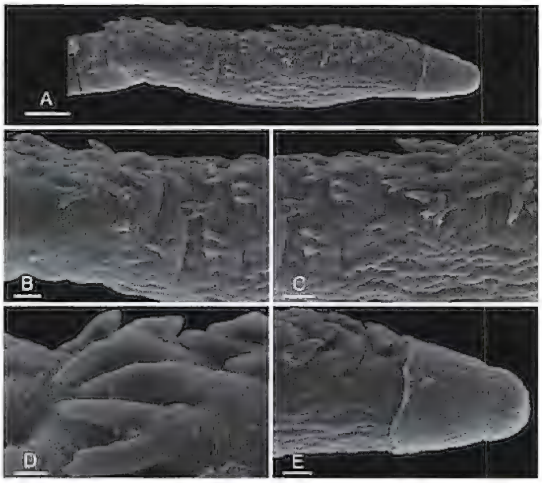

FIGURE 374. *Discodorididae* sp. G, penis, CASIZ 082027. A. Scale = 100 µm.— B. Scale = 30 µm.— C. Scale = 30µm.— D. Scale = 10 µm.— E. Scale = 30 µm.

ilis or an adult *Tayuva lilacina*. However, this specimen is part of a new, unnamed species. Given that the color of the live animal is unknown, it is difficult to say with which species it could be confused based on external morphology. However, the fact that this specimen was misidentified as *Sebadoris nubilosa* suggests that the live animal probably looks like other species such as *lilacina*, *fragilis*, and *nubilosa*, i.e., creamish mottled with brown. We cannot exclude that this species has already been found and misidentified by some workers as *Discodoris concinna*, *Discodoris concin-*

niformis, or *Discodoris fragilis*. However, the literature rarely provides any information on the genital anatomy, so we will never be able to check whether or not this new species was already found. In any case, no valid name seems to exist for it in the existing literature. Its penis can hardly be confused with anything else.

Obviously, further data are needed before we can name this new species. In particular, we need to address the infra-specific variation of several critical features, such as the penial morphology and the color (which is still unknown). Its penis will be an excellent diagnostic character once we know better how it varies among individuals. In order to know the color of the live animal, it will be needed to: 1) take pictures of the collected samples, 2) dissect them, and 3) go back to the color picture if a penis similar to the penis described here is found. This process may take some time.

Supra-specific relationships.— A phylogenetic test of the relationships of sp. G shows that it is part of a large metaphyletic group at the base of *Discodorididae*. Sp. G should be referred to as "*Montereina*" sp. G, under the ICZN, or "*Montereina*" sp. G and *Discodorididae* sp. G, under the *ICPN*.

Species that May or May Not Belong to Discodorididae

The species mentioned below may or may not belong to *Discodorididae*, mainly because, due to a lack of anatomical information, several features were coded as question marks in the data matrix. For all those species, it is therefore difficult to select a generic name as the first part of the Linnaean binomial: given that, under the ICZN, a generic name is required, the genus "*Doris*" is selected here. The quotation marks emphasize that *Doris* may or may not refert o a clade, but is just used here as a default generic name. An alternative nomenclature is also provided, compatible with the *ICPN*, in which *Doridina*, the higher-level taxon that includes all dorids, is used as a clade address, although most of those species likely are cryptobranchs.

"*Doris*" *angulata* (Eliot, 1903) New combination
Doridina angulata (Eliot, 1903) New combination

Peltodoris angulata Eliot, 1903:365-366.

Type material.— The holotype, by monotypy, could not be found.

Type locality.— Chuaka, South-East coast of Zanzibar, western Indian Ocean.

Distribution.— So far, the holotype is the only specimen known.

Remarks on the original description.— The shape of the foot, which Eliot saw as "the most characteristic feature of this specimen," is quite unusual: "[the foot] has a wide margin all round, dilated anteriorly into tentacular expansions, similar to those found in the Aeolididae, and 3.5 millimeters long. The front part seems to be grooved in the middle and the upper lamina to be attached to the head on each side." The tentacles are thin and digitiform. The dorsal notum, minutely granulate, bears two rows of violet-brown spots on each side of the median line, between the rhinophores and the gills. There are six tripinnate branchial plumes. The labial cuticle is smooth; the radular formula is 38 × (45-0-45); all teeth are simply hamate —the innermost teeth are not smaller and the outermost teeth are "not serrulated." The stomach is free and large. Finally, Eliot briefly indicated that he had found "traces of an inconspicuous armature of transparent scales on the glans, but that [he] was not able to satisfactorily make out its arrangement."

Discussion.— Eliot compared *angulata* with two existing species: *Thordisa villosa* (Alder and Hancock, 1864), and *Peltodoris mauritiana* Bergh, 1889, which is a junior synonym of *Peltodoris murrea* (Abraham, 1877) (see this species). The comparison with *mauritiana* probably was motivated by the presence of spots that seemed "to be under the surface and visible through the dorsal skin," which is often as the notum of *murrea* is described. However, Eliot is probably right to write that the presence of innermost teeth of equal size than the other lateral teeth indicate that this specimen is not part of *mauritiana* (i.e., *murrea*). Also, it is true that the absence of *Thordisa*-like papillae on the dorsal notum indicates that this specimen is not a *Thordisa*. The identification of *angulata* is largely based on a problematic feature, i.e., the unusual shape of the anterior foot, which does not vary among discodorids. According to Eliot: "it is clear that the anterior portion of the foot must be expanded in a way unique among the hitherto described species of Dorididae." This suggests that *angulata* may not be a discodorid, despite the thin and digitiform oral tentacles. The absence of illustrations in the original description and the fact that the holotype could not be found prevent us from understanding the exact shape of the foot of the holotype of *angulata*. Therefore, *angulata* is regarded as a *nomen dubium* because both the identity of the species and its classification within *Peltodoris* (and more broadly *Discodorididae*), are doubtful.

"*Doris*" *edwardsi* (Vayssière, 1902) New combination
***Doridina edwardsi* (Vayssière, 1902) New combination**
Figure 375.

Discodoris edwardsi Vayssière, 1902:232-234, plate IX, figs 4-9.

Type material.— Holotype (MNHN, no catalogue number), by monotypy: one specimen 23/14 mm preserved, [leg. *le Talisman* & *le Travailleur* expedition, no collecting date].

Type locality.— Off Cap Ghir, 2 100 m depth, [eastern Atlantic, off Moroccan coasts].

Type material condition.— Vayssière dissected the holotype. The oral area is destroyed. Most internal organs are still present, but poorly preserved and partly destroyed because of Vayssière's dissection. Pieces of the reproductive and digestive systems (including radular teeth and jaws) could be observed.

Distribution.— The holotype is the only specimen known.

Etymology.— Dedicated to Alphonse Milne-Edwards [1835-1900], chief of the *Talisman* expedition.

Remarks on the original description (Fig. 375).— The overall appearance of the body is quite unusual for a *Discodorididae* because the notum is perfectly smooth. Also, the dorsal notum is thin and its lateral edges are narrow (Vayssière wrote that the dorsal notum was continuous with the lateral body wall, as in *Chromodoris*). The color of the live animal is unknown. The preserved specimen currently is homogeneously whitish. Because the oral area was destroyed, the exact position of the oral tentacles could not be determined. Nor could it be determined whether the superior lip of the anterior foot is notched. Actually, only the right tentacle remains and it is difficult to decide whether it is an expansion of the right mouth lip (Vayssière described two 'lateral prolongations of the buccal veil') or if it is an independent tentacle, as in *Discodorididae*. The number of rhinophoral lamellae, not indicated by Vayssière, could not be determined. There are four to six branchial plumes (Vayssière counted five plumes). The original description of the jaws and the radula was confirmed here: there are two jaw plates and the teeth are hamate; however, SEM pictures would probably provide more accurate observations. The cephalic ganglia are not fused. Vayssière's original description of the reproductive system was incomplete. The prostate is tubular and does not seem to be divided in two parts. The duct of the receptaculum seminis was not distinct, but two ducts (vaginal and fertilization) enter the bursa copulatrix, as usual in discodorids. There is an additional duct attached to the proximal end of the bursa copulatrix. This duct seems to be an additional penial organ, although the deferent duct itself could not be seen (probably

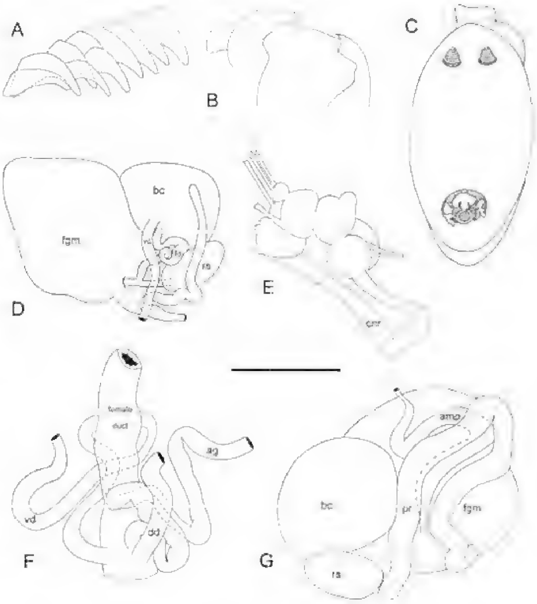

FIGURE 375. *Doridina edwardsi*, holotype. A. Radular teeth (observed in the destroyed buccal mass of the individual, not on a slide), scale = 400 µm.— B. Anterior part of the foot, ventral view, scale = 3.5 mm.— C. Dorsal view, after Vayssière (1902: plate IX, fig. 4), total length = 23 mm.— D. Reproductive system, scale = 3 mm.— E. Nervous system, scale = 1.5 mm.— F. Distal part of the reproductive system, scale = 1.8 mm.— G. Reproductive system, scale = 2.5 mm.

because the connection between the prostate and the penial complex was removed). There seems to be a penial sheath with a papilla inside, but it was not opened and left untouched for future workers who will have access to some additional material.

LITERATURE.— Vayssière (1913), Pruvot-Fol (1954a), Marcus and Marcus (1967a), and Nordsieck (1972) briefly mentioned the existence of *edwardsi* without adding any observations. Pruvot-Fol may have examined the holotype.

DISCUSSION.— More complete observations (radula, jaws, penial complex, etc.) on the single type of *edwardsi* will be more appropriate when additional material is available. Several features, such as the smooth dorsal notum with narrow lateral borders and the organization of the reproductive system, should help people re-identify *edwardsi*. New material, ideally from the type locality (or deep eastern Atlantic waters) is needed.

"*Doris*" *maculosa* Cuvier, 1804
Doridina maculosa (Cuvier, 1804) New combination

Doris maculosa Cuvier, 1804:466-467.— Cuvier, 1817:20-21.— Quoy and Gaimard, 1832:249-250, plate 16, figs 3-5.— Pruvot-Fol, 1934:70-71.
Kentrodoris maculosa.— Bergh, 1878a: II, XXX.— Eliot, 1906b:638, 649-651.
Discodoris maculosa.— Pruvot-Fol, 1935:220-223, fig. 1.

TYPE MATERIAL.— The type material, which likely included only one specimen, could not be found. Pruvot-Fol (1934, 1935) could not find it either.

TYPE LOCALITY.— "Baye des Chiens Marins, côte de la Nouvelle-Hollande," near Dampier's Bay, Western Australia.

DISCUSSION.— The identification of *Doris maculosa* is quite problematic. Indeed, the name *Doris maculosa* was used for two distinct species: Bergh (1878a, 1897) thought that it was a synonym of his *Kentrodoris annuligera* Bergh, 1876, regarded by most authors as a junior synonym of *Jorunna funebris* (Kelaart, 1859); Pruvot-Fol (1935), however, thought that *Doris maculosa* was a *Discodoris*, and that it probably was the same species as *Discodoris sordida* (Quoy and Gaimard, 1832) and *Discodoris fragilis* (Alder and Hancock, 1864). Let us follow history.

Cuvier's original description is extremely brief, just a few lines, with no drawing. It is translated here in its entirety: "It is almost as flat as *scabra*, but half its size and even harder, because the small, short, pointed humps that make its touch harsh, also are sensitive to sight [probably light]. The branchial sheath is not lobed [Cuvier wrote 'point de dentelures,' probably to show a difference with *scabra*, which, being a *Platydoris*, has a branchial sheath deeply lobed]. Its color is dark brown, with irregular, blackish blotches. Mr. Péron found it at la Baye des Chiens Marins, côte de la Nouvelle-Hollande." Because Cuvier did not describe the oral tentacles, we could even doubt that *Doris maculosa* refers to a discodorid (although its similarity with *scabra* suggests that it is a discodorid). Also, with no type material, it is hard to guess what Cuvier actually observed. However, it seems clear that Cuvier's specimen had a dark dorsal surface: dark brown background with blackish blotches. This, as we shall see, is critical information because, although it does not tell us what *Doris maculosa* is, it tells us what *Doris maculosa* is not.

Three decades after the original description, Quoy and Gaimard (1832) identified a new specimen from Vanikoro as *Doris maculosa*. Quoy and Gaimard briefly described the color (my translation): "On each side of the [back of the] body [i.e., each side of the median line], two rows of irregular black patches, on a grey-greenish spooted ground color. The undersurface of the mantle also is spotted with brown patches and dots (...) The foot is red-brown with brown dots." They also mentioned a few external features, such as the presence of small oral tentacles with a yellow tip, and six branchial plumes. This specimen is currently held by the MNHN. After re-examination, it likely is part of the same species as the types of *Doris fragilis*, *Alloidoris hedleyi*, *Doris sordidata*, *Discodoris notiperda*, etc. (see *Sebadoris fragilis*). The tricky question now is: is this specimen part of *Doris maculosa*, i.e., could it be the same species as the (lost) type material of *Doris maculosa* Cuvier, 1804? It surely could. Cuvier died in 1832: although they did not hold a position at the MNHN, Quoy and Gaimard visited it regularly. They knew Cuvier and, thus, could have talked to him about *Doris maculosa*. More importantly, the colors are definitely compatible. The problem is that this compatibility does not prove that the specimen of Quoy and Gaimard from Vanikoro was part of the same unit as the type material observed by Cuvier. Therefore, the safest answer is that those specimens could potentially be part of the same species, but that there is no real evidence to demonstrate it.

Other authors tried to entangle the same question. In the *Uebersicht* of the volume II (part 2) of his *Malacologische Untersuchungen*, Bergh (1878a: p. II) seemed to think that the *Doris maculosa* of Cuvier and Quoy and Gaimard were the same entity, and he still held this view in 1897 (Bergh 1897). Eliot (1906b:651) thought that Quoy and Gaimard's identification was suspicious: "Neither do I feel sure that Quoy and Gaimard's animal from Vanikoro is really identical with either Cuvier's species [*Doris maculosa*] or *K. annuligera*." He expressed similar ideas a year later (Eliot 1907b). Finally, Pruvot-Fol (1934, 1935) thought that Quoy and Gaimard's specimen was distinct from Cuvier's *Doris maculosa*, and she created a new species name for that specimen, *Discodoris vanikoro*. What Pruvot-Fol thought of Cuvier's *Doris maculosa* is quite surprising.

First, Pruvot-Fol (1934, 1935) rightly thought that Cuvier's *Doris maculosa* was not the same entity as *Kentrodoris annuligera* Bergh, 1876, and *Kentrodoris funebris* (Kelaart, 1859). The dorsal color of *annuligera* and *funebris* was described as white or dull yellowish background, with black ring-like irregular blotches. This color, as pointed out by Pruvot-Fol, is hardly compatible with Cuvier's *Doris maculosa*. She also rightly asserted that Quoy and Gaimard's *maculosa* specimen was completely different from *annuligera* and *funebris*. Bergh (1878a, p. II) is the first author who suggested that *Kentrodoris annuligera* Bergh, 1876 might be the same species as *Doris maculosa* of both Cuvier and Quoy and Gaimard. He first suggested this in a small footnote of the *Uebersicht* at the end of the Volume II (part 2), of his *Malacologische Untersuchungen*. Then, a few years later, Bergh (1897) introduced the new combination *Kentrodoris maculosa* (Cuvier, 1804), and regarded his *Kentrodoris annuligera* as the same species as *Doris maculosa* and Kelaart's *Doris funebris*. Eliot (1906b) agreed that *funebris* and *annuligera* were the same species, but he thought that Bergh's interpretation of *Doris maculosa* (both by Cuvier and Quoy and Gaimard) was suspicious. Finally, in her revision of *Jorunna* and *Kentrodoris*, Marcus (1976b) agreed with Pruvot-Fol that *Doris maculosa* should not be regarded as a synonym of *funebris*, (although she accepted the synonymy of *annuligera* with *funebris*).

Second, Pruvot-Fol (1935) thought that Cuvier's *Doris maculosa* was a *Discodoris*, and she created the new combination *Discodoris maculosa*. More interestingly, she also thought that *Discodoris maculosa* was most likely the same species as *Discodoris fragilis* and *Discodoris sordida*. She proposed *Discodoris maculosa* as a valid name for *Discodoris fragilis* and *Discodoris sordida*, but she actually added question marks for both synonyms, because she thought that the synonymies were not certain. Pruvot-Fol's opinion was not based on Cuvier's original description. It was mainly based on a specimen that she found in the collections of the MNHN with a label "*Kentrodoris maculosa* Cuvier." This specimen, she thought, was contemporary of Cuvier, and, she thought too, had probably been identified as *Doris maculosa* by Cuvier himself, before somebody changed the label. Unfortunately, this specimen couldnot be found. In any case, Pruvot-Fol's hypotheses about the history of that specimen are possible but not certain. More importantly, Pruvot-Fol (1935:222, fig. 1f) published a drawing of the distal part of the genital system of that specimen, and she specifically described a distal vestibular gland, which is awkward because *Sebadoris fragilis* (which is what Pruvot-Fol's specimen of *maculosa* was supposed to be) does not have any vestibular gland. There are two hypotheses: 1) Pruvot-Fol made an erroneous observation and she confused the bursa copulatrix with a vestibular gland, in which case her specimen could be part of *Sebadoris fragilis*; 2) Pruvot-Fol made a correct observation, in which case her specimen cannot be part of *Sebadoris fragilis*.

Accepting *Doris maculosa* Cuvier as the valid name for *Discodoris fragilis* (Alder and Hancock, 1864) implied that *Discodoris maculosa* Bergh, 1884 would become a junior homonym of *Discodoris maculosa* (Cuvier, 1804), and thus should have been replaced by a new replacement name (its synonym *Discodoris confusa* did not exist yet). However, the name *Discodoris maculosa* was never used to refer to *fragilis*, except by Pruvot-Fol (1935). Also, authors have continued to use *Discodoris maculosa* Bergh to refer to a Mediterranean species, totally distinct from *fragilis* (see, *Tayuva lilacina*).

Another comment on Pruvot-Fol's (1934, 1935) possible synonym of Cuvier's *maculosa* with *sordida* and *fragilis* needs to be added. Indeed, Quoy and Gaimard's specimen of *Doris maculosa*, which Pruvot-Fol (1934) re-named *Discodoris vanikoro*, is part of *Sebadoris fragilis*, and Pruvot-Fol's *Discodoris vanikoro* is regarded as another junior synonym of *fragilis* (see this species). However, because Pruvot-Fol (1935) also suggested that Cuvier's *maculosa* might be a synonym of *sordida* and *fragilis*, all specimens of *Doris maculosa* (i.e., Cuvier's Australian material, and Quoy and Gaimard's specimen from Vanikoro) could be joined again together in a single entity, as Bergh (1878a) thought, and as Quoy and Gaimard (1832) obviously thought too. This could mean that, as proposed by Pruvot-Fol, *Discodoris maculosa* (Cuvier, 1804) could be the valid name for *Discodoris fragilis* (Alder and Hancock, 1864).

Doris maculosa Cuvier, 1804 is regarded as a *nomen dubium*, which it really is if one considers Cuvier's original description and all the trouble that it generated. Therefore, it is not a valid name for *Sebadoris fragilis*, which is a good thing because the name *Discodoris fragilis* has been used in a large number of publications.

"*Doris*" *noumeae* (Risbec, 1937) New combination
Doridina noumeae (Risbec, 1937) New combination

Peltodoris noumeae Risbec, 1937:159.

TYPE MATERIAL.— The type material, which was probably not deposited in a scientific institution, could not be found. It is probably lost. The number of type specimens is not specified in the original description. The only information provided by Risbec is that he collected and studied the type(s) of *noumeae* between 1929 and 1931.

TYPE LOCALITY.— New Caledonia, [perhaps Noumea].

REMARKS ON THE ORIGINAL DESCRIPTION.— The original description of *noumeae* is brief and largely incomplete. The color is yellow-orange with irregular spots of 'fire-like color.' The liver (black) can be seen by transparency. The rhinophores are yellowish with a white tip. Risbec mentioned that the notum bears spicules, but it seems that Risbec meant 'tubercles' rather than spicules, although it is unclear. The six yellowish gills, transparent, bear irregular opaque white dots. The foot is bilabiate. No notched upper lip was mentioned. The oral tentacles are short and yellowish. The labial cuticle is unarmed. Risbec mentioned twenty hamate teeth per half-row, without specifying the number of rows. The penis is conical.

DISCUSSION.— The name *noumeae* clearly is a *nomen dubium*: many key aspects of its anatomy are unknown (e.g., the exact shape of the oral tentacles, the presence/absence of a notch in the upper lip of the bilabiate foot, the shape of the dorsal tubercles, the number of rows of teeth, the shape of the outermost teeth). Also, the type material could not be found. Risbec (1956) described some specimens of *Peltodoris noumeae* from Vietnam. However, these specimens, which differ from the original description of *noumeae* (e.g., jaws are present) are part of *Sebadoris fragilis* (see this species).

"*Doris*" *patriziae* (Perrone, 1991) New combination
***Doridina patriziae* (Perrone, 1991) New combination**

Figure 376.

Discodoris cf. *stellifera*.— Perrone, 1987:315-321, figs. 1-11 [non *stellifera* Vayssière, 1903]
Discodoris patriziae Perrone, 1991:257-260, figs 1-10.— Costello et al., 2001:202.

TYPE MATERIAL.— Holotype (Stazione di Biologia Marina di Porto Cesareo, Università di Lecce), by original designation: one specimen 16/7 mm alive, leg. A. Perrone, August 1985. There also are two paratypes (not deposited). The type material could not be borrowed, despite several requests. Two letters sent to the Stazione di Biologia Marina di Porto Cesareo remained unanswered, as well as a letter sent to Antonio Perrone's personal address. The type material of *patriziae* is not publicly available.

TYPE LOCALITY.— Radi di Gallipoli (40°02'N, 18°00'E), Gulf of Taranto, [Mediterranean]. The two paratypes were collected from the type locality as well.

ETYMOLOGY.— This species was dedicated to Mrs. Patrizia Candelli.

DISTRIBUTION.— This species is only known from the three type specimens.

REMARKS ON THE ORIGINAL DESCRIPTION (Fig. 376).— The original description of *patriziae* is, as usual with Perrone's work, not good: no color picture of live animals, no SEM pictures, almost no comment on the existing literature, and no consideration for infra-specific variation. However, a few features are commented on. The body is oval. Size ranges from 10 to 16 mm (length) and from 5 to 7 mm (width). The background color is ochre, with two longitudinal rows of three darker blotches on either side of the median line, as well as a few star-like white markings, which host some secretive acidic glands. The dorsal notum bears some large tubercles (which are not caryophyllidia) and some smaller tubercles that are caryophyllidia. The oral tentacles are digitiform. The labial cuticle is armed with rodlets. The radular formula is 10 × (18-0-18). All teeth are described as hamate and all identical, but Perrone does not show all the teeth, either by SEM or through a drawing: he only drew two teeth without specifying whether they were innermost, median, or outermost teeth. The reproductive system was not described.

Discussion.— Perrone published twice the same description of those three specimens from the Gulf of Taranto. He originally thought that those specimens were juveniles of *Archidoris stellifera* Vayssière, 1903. Note that Perrone read Vayssière's (1904) description of *stellifera*, which is not the original description (Vayssière 1903). He then changed his mind and described them as part of a new species. In his discussion, Perrone confidently asserted that *patriziae* was "easily recognizable" with the peculiar dorsal tubercles, the form of the rhinophores, and the dorsal color. Because *patriziae* was easily recognizable, Perrone did not take the time to discuss all the other names proposed in the literature for animals with star-like structures on the dorsum, such as *Discodoris stellifera*, *Geitodoris planata*, and *Doris testudinaria*. He observed a preserved specimen of *planata* sent to him from England, but simply claims that his new species is different from it.

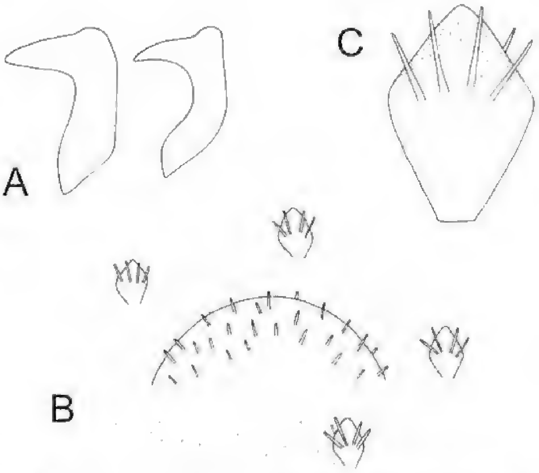

Figure 376. *Doridina patriziae*. A. Two lateral teeth, after Perrone (1991: fig. 10).— B. Dorsal tubercles, after Perrone (1991: fig. 5).— C. Dorsal tubercle, detail, after Perrone (1991: fig. 7).

To say the least, the description of *patriziae* is highly problematic. First of all, it is likely that, as Perrone (1987) first thought, those specimens were young individuals. Many larger (up to 65 mm long) specimens with white, star-like structures on the dorsum have been recorded (both as *stellifera* and *planata*), and with no thorough study of the individual variation of the dorsal color, it is impossible to decide whether or not *patriziae* differs from larger specimens that look alike. Second, the description of the radula is brief, and Perrone's assertion that all teeth are identical is not proved by any SEM picture or drawing, which means that it is not possible to positively say that spatulate, marginal teeth are absent in *patriziae*, which is a critical observation (if *patriziae* were to have such teeth, it would probably immediately become a synonym of *planata*). Third, the rhinophores are totally normal and have nothing special, except, maybe, that they have fewer lamellae (certainly because of the small size of the specimens). Fourth, the description of the dorsal tubercles (large tubercles, which are not caryophyllidia, and in between some smaller caryophyllidia) is extremely ambiguous: it is possible that Perrone interpreted as caryophyllidia some spiculose tubercles. In any case, without SEM pictures or the dorsal notum, the presence of caryphyllidia should not be taken for granted in *patriziae*. Fifth, the reproductive system, which is of primary importance in taxonomy, was not described. It cannot be excluded that the individuals were immature. Sixth, the presence of glands with acidic secretion, if real, strongly suggests that *patriziae* specimens belong to *Geitodoris*, and likely *planata*. The reader shall understand the general spirit of this discussion: *Discodoris patriziae* is regarded as a *nomen dubium* because no type material is available and the original description is incomplete: it will remain extremely difficult to determine what this name refers to.

Supra-specific relationships.— It is not possible to classify *patriziae* mainly because its anatomy is so poorly known. A phylogenetic test of the relationships of *patriziae* shows that *patriziae* does not belong to the clade *Discodoris*, and that it may or may not belong to *Discodorididae*.

“*Doris*” *rubescens* (Bergh, 1905) New combination
***Doridina rubescens* (Bergh, 1905) New combination**

Figure 377.

Peltodoris rubescens Bergh, 1905:134-135, plate III, fig. 12, plate XVI, figs 1-2.— Narayanan, 1971:280.

TYPE MATERIAL.— The holotype, by monotypy, could not be found. It is neither at the ZMA, with the other specimens from the Siboga expedition, nor at the ZMUC, with Bergh's collection. It is probably lost.

TYPE LOCALITY.— Kabaena Island, [SE Sulawesi], station 209 of the Siboga expedition.

DISTRIBUTION.— Only two specimens are known: the holotype, and a specimen collected from the Gulf of Kutch, India (Narayanan 1971).

REMARKS ON THE ORIGINAL DESCRIPTION (Fig. 377).— The holotype measured 28/13 mm, preserved. Its dorsal color was grayish-red with draker spots and a median line of white spots, although it is unclear whether this is the color of the live animal (if Bergh had access to some field notes) or just the color of the preserved animal (which it likely is). The rhinophores and the branchial plumes were white. The body was ovate, with six branchial plumes and rhinophores with 20 lamellae. The foot was rounded anteriorly and posteriorly. Bergh did not mention whether the anterior foot was bilabiate. Nor did he mention whether the upper lip was notched (Bergh usually described this feature). Bergh described tentacles as “small knobs,” but it is unclear whether he was referring to the dorsal tubercles (which he probably was) or the oral tentacles. The labial cuticle was smooth and the radular formula was 24 × (35-0-35). The teeth are simply hamate, with no denticles. The brief description of the reproductive system is not helpful: Bergh simply described an unarmed penis.

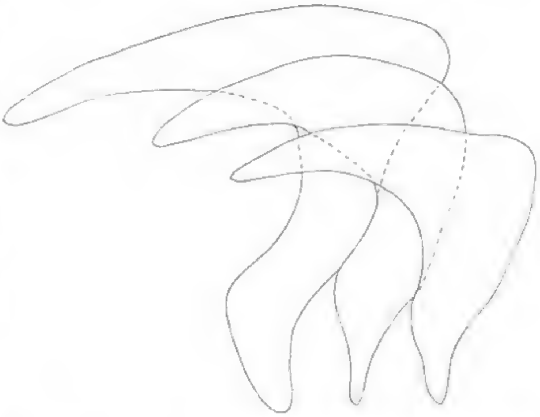

FIGURE 377. *Doridina rubescens*, outermost teeth, after Bergh (1905: plate XVI, fig. 2a).

DISCUSSION.— The drawing of the dorsal color of the animal published by Bergh (1905: plate III, fig. 12) should help people re-identify this species. No specimen could fit with this color pattern. However, whether *rubescens* is a discodorid or not is unclear. The fact that Bergh did not describe the bilabiate anterior foot with the upper lip notched suggests that this species may not belong to *Discodorididae*. However, this is uncertain because Bergh's description of *rubescens* is brief. Finally whether or not the specimen described from India by Narayanan is really part of *rubescens* is unclear because he recognized that it resembled *Peltodoris aurea* Eliot, 1903 as well. Also, the color (cream mantle with yellow margin, and brown papillae) does not fully fit with Bergh's description of the color of *rubescens* (grayish-red background). Probably the only way to address the status of *rubescens* will be to collect new specimens from the type locality.

SUPRA-SPECIFIC RELATIONSHIPS.— It is not possible to classify *rubescens* mainly because its anatomy is so poorly known. A phylogenetic test of the relationships of *rubescens* shows that *rubescens* does not belong to the clade *Peltodoris*, and that it may or may not belong to *Discodorididae*. Supra-specific affinities of *rubescens* could be dealt with once it would be recognized as a species.

"Doris" schmeltziana Garrett *in* Bergh, 1875
Doridina schmeltziana (Garrett *in* Bergh, 1875) New combination

Figure 378.

Doris schmeltziana Garrett *in* Bergh, 1875:228, plate VIII, figs 34-37.
Discodoris schmeltziana.— Bergh, 1877a:519.— Bergh, 1879b: plate V, figs 9-15.— Bergh, 1880a:47-50, plate A, figs 15-19 [Note that part of Bergh's (1880a) re-description of *schmeltziana* refers to *cebuensis*, not *schmeltziana*. This includes Garrett's field notes (Bergh 1880a:48) and Garrett's drawings (Bergh 1880a: plate A, figures 15-19)].— Bergh, 1884a:93.— Eliot, 1910a:422.

Type material (*schmeltziana*).— The type material could not be found. It looks like Bergh thought that his descriptions of *schmeltziana* (original and secondary descriptions) were based on a single specimen, but it seems that he actually observed two distinct specimens. The specific name *schmeltziana* was first published and made available in 1875, under the binomial *Doris schmeltziana* Garrett *in* Bergh, 1875. This new species name is not a *nomen nudum* because it was accompanied by four illustrations of jaw rodlets (Bergh 1875: plate VIII, figs 34-37): according to the Article 12 of the *ICZN*, names published before 1931 do not need to be accompanied by a description in words in order to be available. The number of specimens used in the original publication is unclear, although it seems that only one specimen was dissected by Bergh, in which case the type material should just include a holotype, by monotypy (see discussion).

Type locality (*schmeltziana*).— A brief contribution by J. D. E. Schmeltz (1875), to whom the species is dedicated, tells us that Garrett went collecting in Tahiti. Also, Bergh (1880a) mentions only one locality, the Society Islands, in his re-description of *Discodoris schmeltziana*. So, there is a chance that the specimen of *Doris schmeltziana* whose labial cuticle is illustrated by Bergh (1875) was from the Society Islands.

WWW.— A few pictures of animals identified as *Discodoris schmeltziana* have been posted recently on Bill Rudman's *Sea Slug Forum*. Those specimens should be called *Discodoris cebuensis*, not *schmeltziana*.

Literature.— Dayrat and Gosliner (2005) included *schmeltziana* in a phylogenetic analysis of basal discodorids, but this terminal unit should be called *cebuensis*, not *schmeltziana* (see discussion).

Remarks on the original description (*schmeltziana*, Fig. 378).— The original description of *schmeltziana* is the publication where the name first appeared (Bergh 1875). This description is totally useless, however, except for the fact that we know that *schmeltziana* has a labial cuticle armed with jaw rodlets. A few comments on *schmeltziana* can be added, based on Bergh's (1879b, 1880a) re-descriptions of *schmeltziana*, although we must exclude all information about the dorsal color, which refers to a misidentified specimen that is not part of *schmeltziana* (see discussion): a radular formula of 26 × (37-0-37); all teeth are hamate, with no denticles; a penial papilla (glans) and a praeputium. As Eliot (1910a) pointed out, except for the color, there is not much to say about *schmeltziana*, and given that the color refers to a specimen of *cebuensis*, *schmeltziana* is even less known.

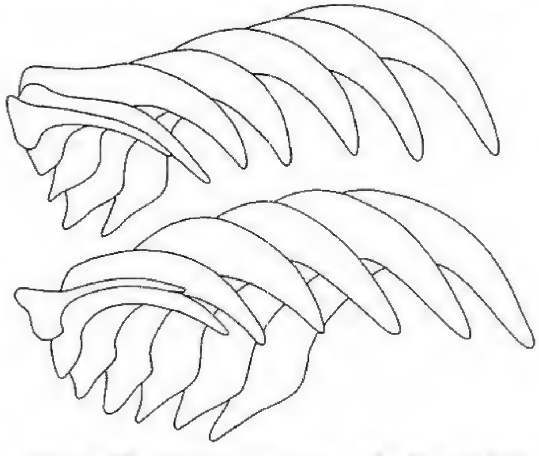

Figure 378. *Doridina schmeltziana*, after Bergh (1879b: plate V, fig. 14).

Discussion.— Although the species name *Doris schmeltziana* was made available in 1875, the species cannot be re-identified based on the original description: labial cuticles are not diagnostic. Two years after the original publication, Bergh (1877a) mentioned "*Discodoris schmeltziana* (Garr.) n. sp." in a list of *Discodoris* species. This was simply a new combination for *Doris schmeltziana* Garrett *in* Bergh, 1875, because the name was already made available in 1875. Bergh (1877a:519) did not publish any figures or written description of *schmeltziana*, but simply indicated in a foot note that: "An investigation of this [*Discodoris schmeltziana*] as well as the *D. crucis* will appear in one of the following notebooks of the Journ. of the Mus. Godefroy." Indeed, two years later, Bergh (1879b) published a few additional figures (radular teeth, dorsal tubercle, nervous system) for "*Discodoris schmetziana* (Garr.)." However, those new drawings were still not accompanied by any text. Finally, Bergh (1880a) published a written description of *Discodoris schmeltziana*, with a few new figures of the external morphology. Bergh (1880a) refers to his previous drawings (Bergh 1875, 1879b) for the internal anatomy.

None of the descriptions of *schmeltziana* published after 1875 can be regarded as the original description. However, if Bergh knew only a single specimen, then all his illustrations and the written description (Bergh 1875, 1879b, 1880a) could be regarded as successive stages of the description of a holotype, by monotypy. The problem is that it seems that Bergh mixed two different specimens that may not even have been part of the same species. One specimen, collected by Garrett from the Society Islands, was 75/35 mm, alive. Garrett made a few drawings of this live animal, some of which were published by Bergh (1880a: plate A, figs 15-19). Garrett also took some field notes about the color of this live animal, which Bergh (1880a:48) published as well. However, Bergh (1880a) also mentioned that he dissected an alcohol-preserved specimen that was 22/18 mm. It is unlikely that this 22/18 mm preserved specimen was the same as the 75/35 mm live animal that Garrett drew.

Therefore, Bergh's (1880a) description was probably based on two different specimens: 1) A live animal drawn by Garrett, for which Bergh (1880a:47-48, plate A, figs 15-19) only described the color and the external morphology; and 2) another specimen, probably also collected by Garrett from the Society Islands, for which Bergh seems to have ignored the color when alive, but for which he described the internal anatomy (Bergh 1875: plate VIII, figs 34-37; Bergh 1879b: plate V, figs 9-15; Bergh 1880a:48-50). Because Bergh only dissected one specimen (the 22-mm long individual), the labial cuticle illustrated in the original description was the labial cuticle of the holotype, by monotypy. As a consequence, the 75-mm long individual should not be part of the type material, and would just be an additional, non-type specimen.

Interestingly, Garrett's drawings published by Bergh (1880a:48, plate A, figs 15-19) are not compatible with Bergh's anatomical description (Bergh 1875: plate VIII, figs 34-37; Bergh 1879b: plate V, figs 9-15; Bergh 1880a:48-50), which supports the hypothesis that Bergh did not dissect the specimen drawn by Garrett in the field, but another specimen. Indeed, based on our current knowledge, all the specimens whose dorsal color is similar to Garrett's drawings (Bergh 1880a: plate A, figs 15-19) are part of *Discodoris cebuensis* (see this species). However, the radular teeth of *cebuensis* are quite different from what Bergh (1879b: plate V, figs 12-14; 1880a:49-50) described, and those differences cannot be the result of individual variation: the innermost tooth of *Discodoris cebuensis* bears a strong, inner denticle, which was found in all specimens, whereas the innermost tooth described by Bergh in *schmeltziana* is smooth; the inner edge of each lateral tooth bears a distinct, pointed spur that corresponds to a wing-like structure present along the inner edge of the tooth foot, whereas this wing-like structure is absent in *schmeltziana*; finally, the two outermost teeth of *cebuensis* have a wide base, and are almost triangular, whereas the outermost teeth described by Bergh are thin and elongated.

Therefore, Bergh's (1875, 1879b, 1880a) descriptions of *schmeltziana* were based on two distinct species: a 22-mm long specimen, preserved, which is the holotype, by monotypy, of *schmeltziana*, because its labial cuticle is illustrated in the original publication (Bergh 1875: plate V, figs 34-37); a 75-mm long specimen, alive, which is part of *Discodoris cebuensis* and which Bergh confused with the holotype of *schmeltziana*.

One thing is clear: *schmeltziana* is not a synonym of *Discodoris cebuensis*, or *vice versa*, even though Bergh included a specimen of *cebuensis* in his re-description of *schmeltziana* along with the holotype of *schmeltziana*, by monotypy. Only the original publication is used to determine the application of a name, and the fact that Bergh published a nice color drawing of a specimen of *cebuensis* in a re-description of *schmeltziana* does not change the fact that *cebuensis* cannot be called *schmeltziana*. It took quite some time to realize that Bergh's (1880a) re-description of *schmeltziana* was based on two specimens that were part of two distinct species and that the color drawings could not be used as a basis for the application of the name *schmeltziana*, which is why the specific name *schmeltziana* was first used instead of *cebuensis* (note that, several records of *cebuensis* have been recently mentioned under the name *Discodoris schmeltziana* on Bill Rudman's *Sea Slug Forum*).

Something is much less clear, however. Indeed, we know that *schmeltziana* should not be used as a valid name for a species that should be called *cebuensis*, but we still do not know what *schmeltziana* really is, and we will probably not find the answer because the anatomical description of *schmeltziana* could potentially apply to many species. Therefore, *schmeltziana* Garrett *in* Bergh, 1875 is regarded as a *nomen dubium*. Interestingly, Eliot (1910a:422) pointed out that *schmeltziana* had been "elaborately described" but that it did "not seem to have any certain characters except the colour." It actually has nothing left because the color is part of a specimen that is not part of *schmeltziana*. Finally, Bergh (1884a) simply mentioned the name *schmeltziana* in a list of *Discodoris* species.

"*Doris*" *stellifera* (Vayssière, 1903) New combination
Doridina stellifera (Vayssière, 1903) New combination

Archidoris stellifera Vayssière, 1903:82-83.— Vayssière, 1904:123-131, plate 4, figs 1-6.— Eliot, 1906e:140.— Eliot, 1906d:339-340.— Eliot, 1910b:99-100.— Vayssière, 1913:315.— Marcus and Marcus, 1967a:69.— Valdés, 2002:603.

Anisodoris stellifera.— Pruvot-Fol, 1951:8.— Pruvot-Fol, 1953:80-81.— Pruvot-Fol, 1954a:240-242, 267, figs 90.— Sordi and Majidi, 1955:239.— Edmunds, 1968b:123, 125, 128, 130.— Schmekel, 1968:115.— Schmekel, 1970:196-197, fig. 57b.— Nordsieck, 1972:62-63, plate O XI, fig. 16.— Ros, 1975:328-329.— Ros, 1976a:57.— Riedl, 1983:337.— Cervera et al., 1985:203.— Ortea, 1990:106.

Discodoris cf. *stellifera*.— Perrone, 1986:26-27, unnumbered figure [as *Discodoris* cf. *stellata*].— Perrone, 1987:315-321, figs 1-11.

Discodoris stellifera.— Thompson and Brown, 1976:132.— Schmekel and Portmann, 1982:84.— Thompson and Brown, 1984:88.— Cattaneo-Vietti et al., 1990:86-87, 224, figs 44-45, plate 5, fig. 6.— Perrone, 1990:299.— Trainito 2003:34, fig. 84.

TYPE MATERIAL.— The type material could not be found. It is not at the MNHN, along with part of Vayssière's collection.

TYPE LOCALITY.— The name *Archidoris stellifera* was first published by Vayssière in 1903, although it is H. von Ihering who actually came up with it. Indeed, in 1891, Vayssière received a note from von Ihering about a new species for which he had found a few specimens in the Gulf of Naples, in the 1880s. This note was an actual description that Vayssière (1904:130) published a year later. According to Vayssière (1904:123), von Ihering invited him to look for this new species in the Gulf of Marseille (Vayssière was a professor in Marseille). Vayssière had already found a few specimens of that species from the Gulf of Marseille between 1877 and 1888. Vayssière then found a few new specimens at the Laboratory of Marine Zoology, Cette (now spelled Sète) near Marseille in March 1903 (note that the year is uncertain because Vayssière wrote "in March of this year," i.e., hypothetically the year of publication). Finally, in the original description, Vayssière (1903) also wrote that this species was commonly found in the spring in the Etang de Thau. In summary, Vayssière wrote his brief original description of *Archidoris stellifera* based on specimens from four different localities: the Gulf of Naples, the Gulf of Marseille, Sète, and the Etang de Thau. Note that the diagnosis published by Vayssière (1903:82), which is the only part of the original description where the species is actually described, seems to have been written by von Ihering, not by Vayssière, and one could regard the Gulf of Naples as the type locality. However, this diagnosis differs from von Ihering's description of *stellifera* published by Vayssière (1904:130). Therefore, Vayssière (1903) may have modified the diagnosis based on his own observations, in which case it is justified to regard all four localities as type localities (the Gulf of Naples, the Gulf of Marseille, Sète, and the Etang de Thau). Future workers will be able to designate a neotype when the taxonomy of *stellifera* is better understood.

Remarks on the original description.— The original description is brief. It consists of a diagnosis that, according to Vayssière, was written by von Ihering, but that Vayssière could have modified based on his own observations. Here is a translation of this diagnosis: "[Dorsal] mantle dark-brown, especially in the median area, with numerous tubercles ['verrucosités']; some of the latter, the largest ones, form pale-yellow stars. Eight bipinnate branchial plumes (sometimes tripinnate). Foot yellowish or orange, with small, dark spots on the edges, as well as upon the inferior side of the mantle. Dimensions: Length from 90 to 110 mm, width from 50 to 60 mm, and height 25 mm." This is not much, just enough to regard *stellifera* as a *nomen dubium*, which would solve a nomenclatural issue (because we would not waste too much time trying to figure out what *stellifera* is), but would not solve a taxonomic issue: How many species with yellow stars on the back are there?

Distribution.— Western Mediterranean (type localities).

Discussion.— To say the least, the taxonomy of *stellifera* is confusing. The first question is whether or not *stellifera* is a synonym of *Geitodoris planata* (Alder and Hancock, 1846). The second question is whether *stellifera* should be classified in *Anisodoris*, *Archidoris*, *Discodoris*, or anything else (assuming that it is distinct from *planata*). Several authors (e.g., Schmekel and Portmann 1982; Thompson and Brown 1984) considered that *stellifera* was just a synonym of *planata*, whereas other authors saw it as a distinct species (e.g., Eliot 1906d; Pruvot-Fol 1953; Cervera et al. 1985; Ortea 1990; Valdés 2002). Unfortunately, no material was available (only a few *planata* specimens). Therefore, the literature is commented on and issues are raised. The literature is confusing because authors may have misidentified *stellifera* specimens as *planata*, and others may have misidentified *planata* specimens as *stellifera*. For that reason, all contributions where the specific name *stellifera* was cited are listed, but the reader should be warned that this bibliographic list is not a list of records for a species '*stellifera*.'

The main source of disagreement about *stellifera* and *planata* (i.e., one *vs.* two species) concerns the yellow star-shaped structures on the dorsal notum: some people thought that those structures were diagnostic of a single species (which most of them called *planata*, although they placed it in different genera); some other people thought that those structures were found in more than one species (i.e., *planata* and *stellifera*). Unfortunately, little information is available about the variation of those yellow star-shaped structures on the dorsal notum, and, more importantly, few authors

(Schmekel and Portmann 1982; Thompson and Brown 1984; Cattaneo-Vietti et al. 1990) have linked precise, dorsal color information (i.e., a color picture or drawing) with anatomical information. The use of the color drawings or pictures accompanied by no anatomy is limited (e.g., Trainito 2003:34, fig. 84, as *Discodoris stellifera*), because it is likely that the two names *stellifera* and *planata* have been used somewhat randomly by authors, and the risks of misidentification are real. So what are we left with? Let us forget about the names for a while and try to figure out how many units there could be (i.e., one *vs.* more than one).

In the literature, one can find two kinds of anatomical descriptions of reddish-brownish animals with yellow stars on the back. Some animals have a radula with spatulate outermost lateral teeth, and an accessory vestibular gland in the reproductive system (e.g., Schmekel and Portmann 1982:71, 84-86, figs 7.10b, 7.15, plate 3, figs 5-7; based on specimens identified as *Discodoris planata* and collected from localities near Naples). Those animals clearly belong to *Geitodoris*, because spatulate marginal teeth are a diagnostic synapomorphy of *Geitodoris*. Several authors also mentioned brownish-reddish animals with yellow stars on the back, but with simply hamate teeth, i.e., with no spatulate outermost lateral teeth. If this anatomical information is correct, then those animals do not belong to *Geitodoris*, and therefore should be part of another species than *planata*. So the combination between the absence of spatulate marginal radular teeth and the presence of yellow stars on the dorsal notum is critical.

Unfortunately, the existence of animals with both non-spatulate, marginal teeth and yellow stars on the dorsal notum is uncertain. In fact, so far, nobody has published a color picture of an animal with a brownish-reddish dorsal notum and SEM pictures of its radula with clearly hamate (non-spatulate), outermost teeth.

In a discussion about *planata* and some of its potential synonyms, Ortea (1990:106) mentions that he observed some specimens from the Mediterranean which look externally like *planata* but which have no spatulate, marginal, radular teeth. However, it seems that he did not describe those specimens in any article.

Cattaneo-Vietti et al. (1990:87) wrote that radular teeth of *Discodoris stellifera* are "all simply hamate." These authors drew four hamate radular teeth (Cattaneo-Vietti et al. 1990: fig. 45). However, they do not indicate the exact position of those teeth in the row, and it seems that they did not draw any of the (potentially spatulate?) outermost teeth because the outermost tooth in their drawing is the largest one (and marginal teeth are usually smaller than the median ones). Also, it is unclear which specimen they used for their drawing. Their drawing of the radular teeth probably was not based on a radula that they mounted but, instead, on a copy of Thompson and Brown's (1984: fig. 18b) drawing of the radular teeth of specimens of *Discodoris planata* from the British Islands. Indeed, the figure 45 published by Cattaneo-Vietti et al. (1990) is close to Thompson and Brown's (1984) figure 18b. More importantly, the other figure published by Cattaneo-Vietti et al. (1990) for *Discodoris stellifera*, the figure 44, which represents the ventral view of the head, is strictly identical to Thompson and Brown's (1984) figure 20b. Interestingly, Thompson and Brown's (1984) figure 18b is supposed to illustrate radular teeth of a *Geitodoris* specimen (although they used the name *Discodoris planata* and although they did *not* draw some spatulate marginal teeth) because: 1) Thompson and Brown developed strong acid-secreting epithelia, which are typically found in *Geitodoris*, and 2) they indicate that the "hook-like teeth [become] degenerate at the margins of the radular ribbon" and that "Schmekel and Portmann (1982) described a radula in which the marginal teeth bear minute serrations," which suggest that they actually observed marginal teeth (although, it is true that the term 'degenerate' teeth is unclear, to say the least).

We also learn from Cervera et al. (1985:203), in a discussion of the non-synonymy between *stellifera* and *planata* that in his Ph.D. dissertation, Ballesteros, in 1980, included a SEM micrograph with a radula of a specimen that he identified as *Discodoris planata* but that Cervera et al. think it was *Discodoris stellifera* (because it apparently was not a *Geitodoris*). However, it seems that this work was not published and is not available. We also learn from Cervera et al. (1985:203) that García first identified a specimen as *Discodoris planata* but that he then re-identified it later (after studying it "fully"!) as *Discodoris stellifera*. Was it because of the radular teeth? Similarly, Pruvot-Fol (1954a) wrote that the radulae of *planata* and *stellifera* are different, but she did not explain how.

Finally, probably one of the most important publications that needs to be commented on is the description of *Archidoris stellifera* that Vayssière (1904) published one year after the original description. This long description is not the original description: it was based on new, additional material from the Gulf of Marseille (three specimens collected in March 1904) and from the Etang de Thau (about 20 specimens collected by the assistant director of the Zoological Station of Cette (i.e., Sète). So, those new specimens were from the type localities but were not the syntypes, which means that Vayssière could have mixed two sympatric species. In any case, his description of the radula of those new specimens is long, but disappointing. Indeed, he ambiguously described the teeth as follows: "The form of the hooks or radular teeth change depending on their position with respect to the rachidian axis, always unarmed; the first teeth, those which are close to the rachidian groove, have a base that is proportionally strong, with a short hook, deeply curved (fig. 6, 1^{e}); then, gradually, when we get farther [away from the rachidian axis], the teeth, while increasing in volume up to the two thirds of each row, present a base proportionally a little bit smaller ['less large' would be the exact translation], but their hook becomes more elongated and becomes less curved. The teeth of the last third [of each hald-row] decrease in volume up to the last one that, usually, is a little bit smaller than the first one and whose shape is slightly modified because of the shortening of the base and the development of the hook." According to Vayssière (1904:128), the radular formula of *stellifera* is: ~19 × (37/46-0-37/46). Interestingly, Vayssière's description of the teeth was accompanied by a drawing with only three teeth, the first, the twelfth, and the thirtieth. All those teeth are hamate: are they hamate because Vayssière observed no spatulate marginal teeth, or because Vayssière simply did not draw the last outermost teeth that could have been spatulate? It is difficut to answer because, again, Vayssière's written description is unclear about the exact shape of the marginal teeth. However, Vayssière drew, for other species, distinctly spatulate, marginal teeth, such as in *Discodoris rubens* Vayssière, 1919 or *Carryodoris joubini* Vayssière, 1919, but those descriptions were published fifteen years after his second description of *stellifera*.

Overall, there is no positive description (with a nice drawing or a clear SEM picture) of spatulate, marginal teeth for an animal with a reddish-brownish dorsal notum with yellow star-shaped structures. All records of such character combination are ambiguous. However, several authors noticed that not all *planata*-looking discodorids have a radula with spatulate, outermost teeth, which means that the teeth of *planata*-looking discodorids definitely should be investigated in greater depth.

If future workers find that a species with a brownish-reddish dorsal notum and hamate marginal teeth actually does exist, then it should be called by *stellifera*. This would be consistent with the literature where most people (who regarded *planata* and *stellifera* as two distinct species) used *stellifera* for such animals. More importantly, this would be compatible with Vayssière's (1904) ambiguous yet unavoidable description of the radular teeth of *Archidoris stellifera*.

Finally, several authors (e.g., Eliot 1906d; Pruvot-Fol 1954a; Schmekel and Portmann 1982; Cervera et al. 1985) discussed the possibility that the valid name for *stellifera* could be *Doris testudinaria* Risso, 1818 (note that by "*stellifera*," some authors actually refered to *planata* though). Eliot (1906d) thought that *Archidoris stellifera* was a synonym of *Archidoris testudinaria*, which he regarded as a species distinct from *Geitodoris planata*. However, Eliot gave the erroneous authorship "(A. & H.)" for *Archidoris testudinaria*. As pointed out by Pruvot-Fol (1954a), the author of *Doris testudinaria* is Risso (1818) and nobody else. Vayssière (1913) thought that his *Archidoris stellifera* was a synonym of *Archidoris testudinaria*, although he gave a wrong date of original description (i.e., Risso 1826, instead of Risso 1818). It is unclear whether he thought that only Risso (1826) could refer to *stellifera*, and not Risso (1818). Pruvot-Fol (1936a, 1936b, 1954a) already pointed out that Risso's (1818) original description of *Doris testudinaria* was not informative, and its identification too uncertain. *Doris testudinaria* Risso, 1818 is regarded as a *nomen dubium* (see this species).

It is possible that if two units are recognized (*planata* and *stellifera*). then other morphological and anatomical differences will then be discovered, such as for the penial shape, the number of gills, and, even, some non-overlapping individual color variation.

Supra-specific relationships.— Addressing the supra-specific affinities of *stellifera* is tricky, because its anatomy is still largely unknown. In fact, a phylogenetic test of the relationships of *stellifera* shows that it may or may not belong to *Discodorididae*. It cannot be positively classified within any of the genera proposed so far.

Based on Vayssière's (1904) description (which, again, is not the original description), *stellifera* should belong to *Discodorididae* because of the presence of the digitiform oral tentacles and the notched upper lip of the anterior, bilabiate foot. Therefore, it probably should not be classified in *Archidoris*. What are the other choices?

Most authors used the combination *Anisodoris stellifera*. Some of them (e.g., Pruvot-Fol 1951, 1953, 1954a) meant to refer to something different from *planata*, and some others (e.g., Schmekel 1970) referred to *Geitodoris planata*. Marcus and Marcus (1967a) briefly stated that *Archidoris stellifera* was "certainly not an *Anisodoris*," but they did not propose an alternative. The combination *Discodoris stellifera* was also used by several authors (e.g., Perrone 1986, 1987; Cattaneo-Vietti et al. 1990; Trainito 2003) although the synonymy of *Anisodoris stellifera* with *Discodoris planata* proposed by Thompson and Brown (1976, 1984) implied that *stellifera* was another nominal species of *Discodoris*. Finally, according to Valdés (2002:603), *stellifera* "should be placed in a genus of caryophyllidia-bearing dorids." This statement, however, was based on Perrone's (1987) re-description of three specimens of *Discodoris* cf. *stellifera*, for which, by the way, he created the new species name *Discodoris patriziae* in 1991 (see this species). Perrone (1987) did mention caryophyllidia and drew a tubercle that could be interpreted as a caryophyllidium. However, the low quality of Perrone's descriptions makes any of his statements doubtful. The presence of caryophyllidia on the dorsal notum of something called '*stellifera*' is possible, but should certainly be addressed in the future.

"*Doris*" *testudinaria* Risso, 1818
Doridina testudinaria (Risso, 1818) New combination

Doris testudinaria Risso, 1818:370-371.— Risso, 1826:33, fig. 15.— Delle Chiaje, 1822: plate 38, fig. 8.— Philippi, 1836:104.— Philippi, 1844:78.— Alder and Hancock, 1862:261-262.— Alder, 1869:85.— Colgan, 1914:196-197 [with an erroneous authorship "Ald. & Hanc."].— Pruvot-Fol, 1936a:532.— Pruvot-Fol, 1936b:634-635.— Pruvot-Fol, 1951:8, 14.— Verany, 2001:53-54, plate 2, fig. 12n-12p.

Archidoris testudinaria.— Eliot, 1906d:339-344.— Walton, 1908:238.— Eliot, 1910b:99-104, plate 1, figs 5-8.— Vayssière, 1913:315, 317 [Eliot and Walton cite an erroneous authorship: "Alder and Hancock"].

Anisodoris testudinaria.— Pruvot-Fol, 1953:80.— Pruvot-Fol, 1954a:240.— Ros 1975:328.

Geitodoris testudinaria.— Valdés, 2002:600.

Discodoris testudinaria.— Thompson and Brown, 1976:132.— Schmekel and Portmann, 1982:84.— Thomp-

son and Brown, 1984:88 [Thompson and Brown cite an erroneous authorship: "Alder and Hancock, 1862"].
Platydoris testudinaria.— Eliot, 1906d:341.

Type material.— The type material could not be found, and is probably lost.

Type locality.— Off Nice, Mediterranean [collected in February, rocks].

Remarks on the original description.— The original description (Risso 1818) is quite brief. It is translated here in its entirety: "Ovate body, convex above, covered with a large notum free on both sides, tuberculated and blackish in the middle, dark brown on the edges where it bears pale yellow lines which form small, regular polyhedra. Tentacles (certainly the rhinphores) subcylindrical, yellowish. Five gills, pinnate, dentate, purplish, with pale yellow lines. Inferior surface of the body and foot of a beautiful dark orange color. Long copulatory [reproductive] organ, cylindrical, ending in a small, sharp, apex, located in the middle of the right lateral side." In addition, Risso gives a length ranging from 70 to 76 mm and a width ranging from 45 to 48 mm.

Discussion.— *Doris testudinaria* Risso, 1818 is another example of those early names (see, e.g., *Doris maculosa* Cuvier, 1804, and *Doris granulata* Ehrenberg, 1831) for which it is difficult to know which species they actually refer to, especially when there is no type material available, because the original description was vague or brief (usually both). The general consensus in the literature is that the identification of *Doris testudinaria* is problematic (e.g., Pruvot-Fol 1936a, b, 1954a) and people who cited this name as a synonym often added a question mark in order to show that the synonymy was hypothetical (e.g., Pruvot-Fol 1954a; Schmekel and Portmann 1982; Valdés 2002), hence its status of *nomen dubium* here. The bibliographic list of references above simply serves the purpose of providing the reader with a list of contributions where the specific name *testudinaria* is cited, but it certainly does not imply that all those authors refer to the same species.

Some authors (e.g., Schmekel and Portmann 1982) thought that Delle Chiaje's (1822) *Doris testudinaria* might have been a misidentification of *Archidoris pseudoargus* (von Rapp, 1827). This is possible, but since it is not an original description, it does not really matter. Pruvot-Fol (1951) thought that Delle Chiaje's (1822) *testudinaria* could be a synonym of *Discodoris indecora* Bergh, 1881, now *Paradoris indecora* (see this species), and she also thought that Alder and Hancock's (1862) and Eliot's (1910b) *testudinaria* were a misidentification for *Anisodoris stellifera* Vayssière, 1903 (see *stellifera*).

Alder and Hancock (1862) thought that Risso's *Doris testudinaria* and their *Doris planata* were distinct species. Note, however, that Alder and Hancock referred to Risso's (1826) illustration of *testudinaria*, and not the original description published earlier, in 1818. A few years later, Alder (1869) thought that both names were synonymous, and regarded *Doris testudinaria* as the valid name. This means that *Doris testudinaria* could potentially be the same species as *Geitodoris planata*, which, again, is possible. Several authors agreed with this interpretation (e.g, Schmekel and Portmann 1982; Valdés 2002). Cervera et al. (1985) briefly stated that Alder and Hancock's (1862) and Alder's (1869) *testudinaria* probably are the same species as *Geitodoris planata*, but they did not comment on Risso's *testudinaria*.

Bergh (1877a:498) thought that both Risso's (1826) and Philippi's (1836, 1844) *Doris testudinaria* were misidentifications of *Platydoris argo* (Linnaeus, 1767). This, again, is possible. However, Alder and Hancock (1862) thought that Philippi's (1844) *Doris testudinaria* was the same species as Risso's *testudinaria*, which Alder (1869) regarded as the valid name for their *Doris planata*.

Eliot (1906d) thought that the specimen of *testudinaria* described from Herm Island by Alder and Hancock (1862), as well as Risso's (1826) *testudinaria* (with a question mark though) were the same species as Vayssière's *Archidoris stellifera*, hence the new combination *Archidoris testudinaria*, and were all different from *Geitodoris planata*. Vayssière (1913) agreed with Eliot (1906d) and actually used *Archidoris testudinaria* as the valid name of *Archidoris stellifera*. Note, however, that both Eliot and Vayssière did not reach their conclusion based on Risso's (1818) original description, and, as pointed out by Pruvot-Fol (1936a, 1936b, 1954a), it is unclear whether both of Risso's (1818, 1826) *testudinaria* are part of the same species. In any case, as rightly pointed out by Pruvot-Fol (1954a) again, the authorship of *Archidoris testudinaria* cannot be "Alder and Hancock," as suggested by Eliot (1906d, 1910b). Eliot's (1910b) views on *testudinaria* are similar to Eliot's (1906d) views. However, Eliot's (1910b) contribution is important, however, because he published two of Hancock's drawings (not including the dorsal surface) for the specimen from Herm Island identified as *Doris testudinaria* by Alder and Hancock (1962). The drawing of the dorsal surface published by Eliot (1910b: plate 1, fig. 5) illustrates a specimen from Plymouth and identified as *testudinaria* by Eliot himself. It is, indeed, similar to the drawing published by Vayssière (1904) for the dorsal surface of *Archidoris stellifera*.

Pruvot-Fol (1954a) saw Risso's (1818, 1826) *Doris testudinaria*, which she named *Anisodoris testudinaria*, as a possible synonym (with a question mark though) of *Anisodoris stellifera*, a species she thought was distinct from *Geitodoris planata*. Colgan (1914) regarded "*Doris testudinaria* (Ald. & Hanc.)" as a species distinct from *Doris planata*. It is possible that the specimens (from Irish coast) that Colgan looked at were part of *planata*. Ros (1975) agreed with Pruvot-Fol about the the fact that *testudinaria* was a possible synonym of *stellifera*, although unlike Pruvot-Fol he also mentioned in the list of synonyms of *Anisodoris stellifera* some publications that clearly refer to *Geitodoris* specimens, such as Alder and Hancock's (1862) *Doris testudinaria*. Thompson and Brown (1976, 1984) regarded Alder and Hancock's *Doris testudinaria* as a name used for *Discodoris planata*, but they did not comment on Risso's *testudinaria*. Cattaneo-Vietti et al. (1990) regarded Alder and Hancock's *Doris testudinaria* as a name used for *Discodoris stellifera*, but they did not comment on Risso's own *testudinaria*. There is no need to insist on the ambiguity between *stellifera vs. planata* (see *stellifera* for a discussion). The point here is that authors have already proposed *testudinaria* as a potential synonym of *stellifera*. Interestingly, a manuscript written by Vérany during the 1850s, but published only recently (Vérany 2001) includes a color drawing of a specimen he identified as *Doris testudinaria* Risso, and that is similar to Vayssiére's (1903) drawing of the dorsal color of *stellifera*.

This confusion over the identity of *Doris testudinaria* Risso is largely the result of the fact that the original description was extremely vague. Also, the problematic separation between *stellifera* and *planata* did not help. Finally, the fact that some authors did not understand the distinction between taxonomy and nomenclature certainly participated in increasing the confusion: e.g., regardless of the species which Alder and Hancock's (1862) specimens identified as *Doris testudinaria* are part of, the author of *Doris testudinaria* remains Risso (1818).

SUPRA-SPECIFIC RELATIONSHIPS.— A phylogenetic test of the relationships of *testudinaria* (based on the original description) shows that it may or may not belong to *Discodorididae*, and therefore cannot be placed in any of the discodorid genera, such as *Discodoris*, *Anisodoris*, or *Geitodoris*.

"*Doris*" *timorensis* (Bergh, 1905) New combination
***Doridina timorensis* (Bergh, 1905) New combination**
Figure 379.

Anisodoris timorensis Bergh, 1905:97-98, plate XII, fig. 33-35.

Type material.— The holotype, by monotypy, could not be found. It is neither at the Zoölogisch Museum, Amsterdam, with the other specimens from the Siboga expedition, nor at the ZMUC, with Bergh's collection. It is probably lost.

Type locality.— Northeastern point of Timor (Siboga St. 282), by 25-30 meters depth.

Distribution.— The holotype is the only specimen known.

Remarks on the original description (Fig. 379).— The animal, likely preserved, measured 20/16 mm. Its dorsal color was grey, with a reddish-dotted margin, and with whitish rhinophores and gills. The oral tentacles are 'small lobes,' which may or may not be digitiform. The anterior foot is described as bilabiate and 'crenate in the middle,' which may refer to a notched upper lip or some projections of the anterior foot. Bergh mentioned five branchial plumes. The radular formula given by Bergh was 39 × (45-0-45), with strongly denticulate teeth. The reproductive system was not described.

Discussion.— The identification of *timorensis* will certainly remain a challenge for quite some time because the type is likely lost, because Bergh did not publish a drawing of the dorsal color, and because the original description is vague. Therefore, this name is regarded as a *nomen dubium*.

Supra-specific relationships.— The uncertainty on whether oral tentacles are digitiform or not and whether the anterior foot is notched or not suggests that *timorensis* may not belong to *Discodorididae*. Bergh admitted that determining the generic affinities of that species was hardly possible, and tentatively placed it in *Anisodoris*. A phylogenetic test of the relationships of *timorensis* (based on the original description) shows that it may or may not belong to *Discodorididae*.

Species that Do Not Belong to Discodorididae

"*Doris*" *prea* (Marcus and Marcus, 1967) New combination
Doridina prea (Marcus and Marcus, 1967) New combination

Figures 380-381.

Anisodoris prea Marcus and Marcus, 1967a:70-72, figs 90-93.— Eyster, 1980:582-588, figs 1, 2A-B.
Atagema prea.— Thompson, 1980:86-87, figs 7-9.

Type material.— Four syntypes (NMNH 576278): four specimens 28/17 (#1), 28/17 (#2) [dissected for the present study], 25/15 (#3) [dissected by the Marcus], and 17/9 (#4) mm preserved, leg. F. Bayer, [21 February 1948].

Type locality.— Matheson Hammock, Biscayne Bay, Florida.

Type material condition.— One syntype (#3) was dissected by Ernst and Eveline Marcus. The slides with the radula and the reproductive system could not be found and are probably lost. The three other syntypes were well preserved. One of them (#2) is described here.

Habitat.— The four syntypes were found on *Thalassia* and sand bottom. The specimen collected by Thompson was found in a coral boulder (3 meters depth). Eyster collected her 17 specimens of *prea* on a white sponge in a deep muddy creek.

Distribution.— Florida (type locality), and probably Jamaica (Thompson 1980) and South Carolina (Eyster 1980).

Remarks on the original description (Fig. 380E).— The color of the live animals is

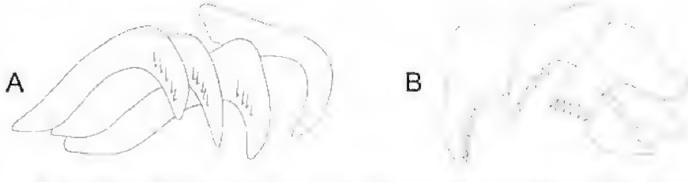

Figure 379. *Doridina timorensis*. A. Lateral teeth, after Bergh (1905: plate XII, fig. 33).— B. Outermost teeth, after Bergh (1905: plate XII, fig. 35a).

unknown. The preserved syntypes are all homogeneously whitish. The notum is covered with "low, flat knobs of different size, each big one surrounded by a number of small ones." Those tubercles are not caryophyllidia. The middle of the back is nearly smooth, and bears no tubercles. The Marcus mentioned about 30 rhinophoral lamellae, but only 15 (#4) and 22 (#1) lamellae were found (lamellae could not be counted in the two other syntypes). There are from six to eight multipinnate branchial plumes (the Marcus counted seven plumes). The anterior foot is bilabiate. However, contrary to what the Marcus described, the upper lip is not notched. The labial cuticle is smooth. The radular formula is 25 × (29/30-0-29/30) in a 25 mm long specimen. The teeth are hamate, with no denticles. The prostate is "much longer than wide." The deferent duct is convoluted, with several tight loops. There is a short penial papilla, which is probably not a distinct, permanent, copulatory organ. The bursa copulatrix is six times larger than the receptaculum seminis. Both pouches are spherical.

Description of a syntype (Figs. 380-381).— *Color*. The color of the live animal is unknown. The preserved animal is homogeneously whitish.

External morphology. The length equals less than twice the width. The foot is rounded posteriorly and anteriorly. The anterior margin of the foot is bilabiate (although the groove is weak), but the upper lip is not notched. The two oral appendages correspond to lateral expansions of the mouth lips. They are flattened, not grooved. The notum is covered with rounded elevated tubercles of (mainly two) different sizes: large tubercles surrounded by smaller tubercles. Two longitudinal rows of bigger tubercles run from the rhinophores up to the gill opening. Small holes (diameter < 10 μm) seem to be present on the surface of the mantle. Tufts of cilia are present on the dorsal notum, but rare. The margins of the rhinophoral sheaths and branchial pockets are lightly crenulate. There are eight tripinnate gills arranged in circle around the anus. The Marcus described seven gills, but some vestigial gills are sometimes difficult to see.

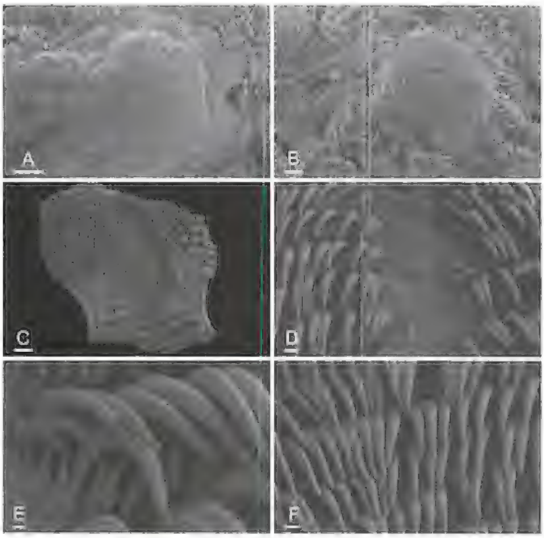

FIGURE 380. *Doridina prea*, syntype, NMNH 576278 (#2). A. Dorsal tubercles, scale = 200 μm.— B. Dorsal tubercles, scale = 100 μm.— C. Radula, scale = 200 μm.— D. Innermost teeth, scale = 30 μm.— E. Outermost teeth, scale = 10 μm.— F. Median teeth, scale = 30 μm.

Internal Anatomy. The stomach is free, on top of the left side of the digestive gland. The intestine is straight and dorsal. The labial cuticle is smooth. The radula is about one and a half times longer than wide. The radular sac cannot be seen by dorsal dissection. The radular formula is 19 × (33-0-33) in a 28 mm long specimen. Rachidian teeth are absent and the rachidian space is narrow. The lateral teeth are at an angle of 90 degrees with the rachidian axis. The size of the lateral teeth is globally constant except for the eight innermost teeth whose size gradually increases, and the five to eight outermost teeth whose size gradually decreases. All teeth are simply hamate, except for the outermost tooth, which is straight due to its reduced size. The teeth bear no denticles, nor are they grooved.

Nervous system. The circum-esophageal nerve ring is short, i.e., its length equals the width of the dorsal cerebro-pleural ganglia. The cerebral and pleural ganglia are fused and cannot be distinguished. There is only one blood gland. However, it was clearly posterior to the cephalic ganglia and there might be two blood glands.

Reproductive system. The reproductive system is located on the right side of the body, between the buccal mass and the digestive gland. The ampulla is straight. The division between male and female ducts could not be seen by dissection. The prostate is clearly tubular. The transition between the prostate and the deferent duct is unclear. No distal accessory gland and no penial papilla were found. The vaginal duct is convoluted, with a few loops from the common atrium to the bursa copulatrix. The latter is about twice as large as the receptaculum seminis. The fertilization duct is short, straight from the bursa copulatrix to the female gland mass. The duct of the receptaculum seminis is also short. The organization of the spermatic ducts is semi-serial.

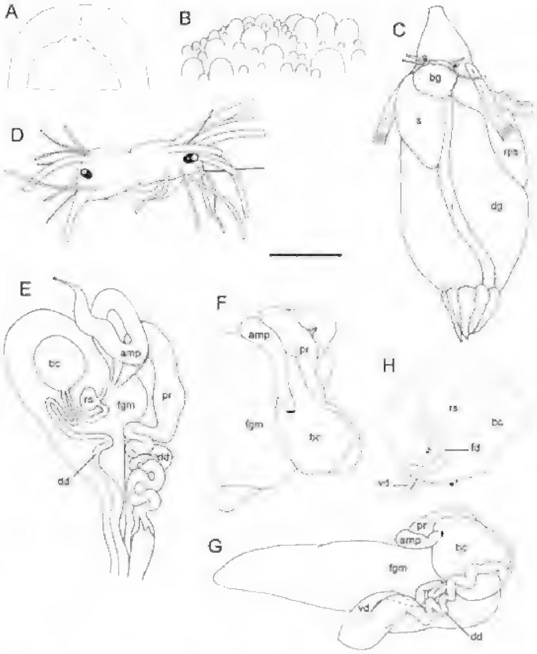

FIGURE 381. *Doridina prea*, syntype, NMNH 576278 (#2) except E. A. Anterior, ventral view, scale = 7.5 mm.— B. Dorsal tubercles, scale = 2 mm.— C. General anatomy, scale = 3.5 mm.— D. Nervous system, scale = 1.4 mm.— E. Reproductive system, after Marcus and Marcus (1967a: fig. 93).— F. Reproductive system (female gland mass not entirely represented), scale = 5.3 mm.— G. Spermatic pouches (prostate removed), scale = 3.4 mm.— H. Reproductive system, scale = 5 mm.

DISCUSSION.— After the first record from Florida, *prea* was found in Jamaica (Thompson 1980) and South Carolina (Eyster 1980). Thompson collected one specimen and Eyster collected 17 specimens. Both authors observed live animals and described similar colors for the dorsal notum: brown background with darker and white spots. Eyster noticed some variation depending on the size of the specimens though (larger specimens being darker). The descriptions provided by Thompson and Eyster are compatible with the anatomy of the syntypes of *prea* and those records are regarded as valid in the present study. Both Thompson and Eyster pointed out the presence of small and large tubercles on the dorsal notum. Thompson observed a "strongly tuberculated" mid-dorsal area, which differs from the original description, but this difference could be infra-specific. Thompson described "flattened oral lobes but no tentacles" and Eyster described "small, flat, blunt, and lobe-like" oral tentacles. Thompson described a bilabiate anterior foot. He did not specifically mention whether the upper lip of the anterior foot was notched, but it likely was not notched because for the next species in his paper (*Atagema browni*), he did mention a notch either. Unfortunately, Eyster did not describe the anterior foot. Radular formulae are compatible with the Marcus' description and new observations: 29 × (48-0-48) in a 30 mm long specimen (Thompson 1980), 23/29 × (32/43-0-32/43) in a 33 mm long specimen, and 15/19-0-15/19 (number of rows unknown) in a 6 mm long specimen (Eyster 1980).

All those specimens from Florida (types), Jamaica, and South Carolina probably belong to the same species (based on similarity of the dorsal tubercles and the radula). There is no reason to think that they are part of a different species, although more material is needed, and especially a better study of the penial structure and the color variation.

SUPRA-SPECIFIC RELATIONSHIPS.— Based on re-examination of the syntypes, it seems that *prea* is not a discodoridid: it lacks several synapomorphic features of discodorids, especially the digitiform oral tentaclesand the notched upper lip of the anterior foot. Therefore, it cannot be classified within *Anisodoris* or *Atagema*. A phylogenetic test of the relationships of *prea* shows that it does not belong to *Discodorididae*.

Future studies.— Whether *prea* is a valid name or a synonym could not be addressed here. This question will require to sample other similar species in Dorididae. Collecting new specimens from the type locality (Biscayne Bay, Florida) would probably be necessary if we want to know the color (and the external morphology) of live animals from the type locality. This would help determine with more certainty whether or not the specimens described by Eyster and Thompson are really part of *prea*. Addressing the supra-specific relationships of *prea* will also require sampling other similar species, likely in dorididae.

"*Doris*" *versicolor* (Bergh, 1905) New combination
Doridina versicolor (Bergh, 1905) New combination

Figure 382.

Discodoris ?? *versicolor* Bergh, 1905:108-110, plate IV, fig. 1, plate XIV, figs 29-31.

Type material.— Holotype (ZMA Moll 3.05.151), by monotypy: one specimen 55/40 mm preserved, leg. Siboga Expedition, 18 December 1899.

Type locality.— Great Kei Island, West coast, 27 meters depth (dredge), Elat, Indonesia (station 261 of the Siboga Expedition).

Type material condition.— The holotype was entirely dissected by Bergh. The body wall is globally well preserved. No internal organs remain except for the digestive gland (cut in two half).

Distribution.— The holotype is the only specimen known.

Habitat.— Mud, reef.

Remarks on the original description (Fig. 382).— The preserved color is homogeneously light yellowish. The anterior end of the foot is bilabiate but the superior lip is not notched. There are no oral tentacles (possible mouth lip expansions may have been cut with the oral area). The dorsal surface of the notum does not bear any tubercles, but bears large, flattened humps, as in *Asteronotus cespitosus*. There are five branchial plumes, surrounded by a smooth branchial sheath. The notum seems to contain no spicules. The labial cuticle is armed with jaw rodlets. The radular formula is 140 × (125-0-125), which is quite high. Teeth are hamate, smooth.

Discussion.— This specimen is not a discodorid. It may belong to *Actinocyclus*, although it is uncertain, especially given the number of branchial plumes described by Bergh: *versicolor* is regarded as a *nomen dubium*.

Supra-specific relationships.— A phylogenetic test of the relationships of *versicolor* confirmed that *versicolor* does not belong to *Discodorididae*.

COMMENTS ON *DISCODORIS* AND *PELTODORIS* SPECIMENS MENTIONED IN IHE LITERATURE WITHOUT SPECIFIC NAME (ARRANGED BY DATE)

Discodoris sp. Bergh, 1905:110-111, plate XIV, figs 32-36.— Bergh rarely considered that he did not have enough data to create a new species name, which means that when he described specimens without naming them, it is probably that he had almost no information. It is impossible to determine what Bergh observed because the features that he described for this *Discodoris* sp. are general. The specimen described by Bergh is neither at the ZMA (with the rest of material from the Siboga expedition) nor at the ZMUC (with the Bergh's own collections).

Discodoris sp. Eliot, 1906e:139, plate XIV, fig. 3.— It seems that the two specimens described from the Cape Verde Islands as *Discodoris* sp. do not belong to *Discodorididae*.

Peltodoris sp. Eliot, 1906e:143.— Eliot decided not to name this 12 mm long animal from Cape Verde Islands because he thought it was immature. The live animal was yellow, with red-brown gills. According to Eliot, the dorsal notum was similar to the notum of *Rostanga evansi*, a species re-allocated to *Jorunna* by Rudman and Avern (1989), which means that maybe this *Peltodoris* sp. had some caryophyllidia. However, Eliot found a bilabiate "apparently not notched," anterior foot, which means that maybe this specimen was not a *Discodorididae*.

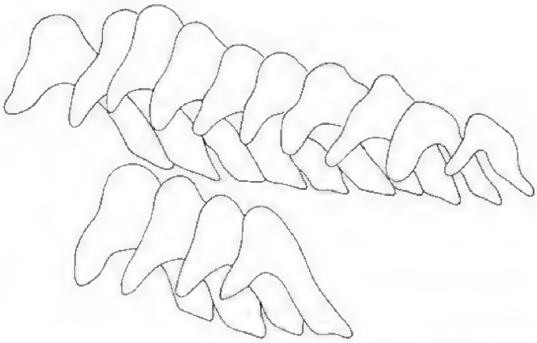

FIGURE 382. *Doridina versicolor*, outermost teeth, after Bergh (1905: plate XIV, fig. 31).

Discodoris sp. Eales, 1938:100.— This 7/4.5 mm specimen, collected off the South Arabian coast, at 30 meters depth, during the John Murray expedition, could not be found. The color of the live animal was unknown. The preserved specimen was colorless. The finger-like tentacles (and the "bifid"anterior end of the foot) indicate that this animal belongs to *Discodorididae*. The labial cuticle is unarmed. The radular formula is 42 ´ (63-0-63) but "the teeth are so small and close together that it is difficult to count them." This is a problem often faced with *Rostanga* species, which would fit with Eales's description of the lateral teeth: "All the laterals are hooked and have a smooth edge. The innermost are broad and shortly hooked, the outermost long and slender, and hardly hooked at all but merely curved slightly." However, Eales wrote that this description "agrees fairly closely with Bergh's *D. boholiensis*," which clearly is not a *Rostanga*. In conclusion, it is difficult to identify what Eales's *Discodoris* sp. is.

Discodoris sp. Pruvot-Fol, 1953:76.— This 60 mm long specimen collected from Dakar, Senegal, clearly belongs to *Discodorididae* (because of the presence of an bilabiate anterior foot with an upper lip notched and digitiform oral tentacles). Its (preserved) color is described as "homogeneously grey, with brown spots (dots) on the dorsal and ventral sides." Ortea et al. (1981) thought that Pruvot-Fol's description indicated that this specimen could be part of *Discodoris fragilis*. It probably is not part of *fragilis*, which is distributed in the tropical Indo-West Pacific and has not been found in Atlantic. However, Ortea used *Discodoris fragilis* to refer to a *Tayuva* species. The specimen described by Pruvot-Fol could be part of a *Tayuva* species, but it could also be anything else.

Discodoris sp. Pruvot-Fol, 1954b:14-16, fig. 4.— Pruvot-Fol described a few features of two specimens from Hikueru, Tuamotu, French Polynesia. However, as she points out in her description, it is difficult to determine what those animals were or were not, especially because of the complete absence of information about their color, when alive. At least, we know that those two specimens belong to *Discodorididae* (because of the presence of digitiform oral tentacles).

Peltodoris sp. Vicente, 1966:111-114, plate XIV.— Although it is accompanied by a few drawings, Vicente's description of this 10 mm long specimen, collected from Tuléar, East coast of Madagascar, is vague. The animal was black with numerous white blotches, lightly bluish. However, it is unclear whether or not this specimen belongs to *Discodorididae* because Vicente did not describe the oral area (anterior foot and oral tentacles).

Discodoris sp. Lim & Chou, 1970:99, figs 1F, 3L, 4L, 7A-B.— Lim and Chou (1970:104) actually identified those specimens as *Discodoris annuligera* in an addendum for that paper.

Discodoris sp. Behrens, 1980:102, fig. 149.— It is the same picture as *Discodoris* sp. 1 Behrens, 1991. It is unclear whether this pure white, 18 mm long animal, collected off Malibu, southern California, belongs to *Discodorididae* or not, because it is described as similar to *Archidoris odhneri*.

Peltodoris sp. Behrens, 1980:102.— Actually spelled as *Peltadoris*. This is part of *Peltodoris mullineri*.

Discodoris sp. Orr, 1980:113.— Numerous specimens were described briefly in three lines: their rhinophores are smooth "apart from a few lamellae at two dorsal end," and the mantle is "dull orange/brown with black spots." It is impossible to determine what Orr was referring to.

Discodoris sp. Orr, 1981:45, unnumbered figure.— This 21 mm long animal, from Hong Kong, cannot be identified because the picture is too fuzy. The dorsal color is "pale beige or olive bearing brown patches and spots which are partly obscured by numerous hair-like tubercles." The radular formula is 13 ´ (16-0-16) but this does not tell us much.

Discodoris sp. 1 Gosliner, 1987:64, fig. 75.— This animal was recently identified as *Paradoris erythraeensis* (Vayssière, 1912), although it is still unclear at this stage whether *erythraeensis* refers to one polymorphic single unit or multiple entities (Dayrat 2006). Camacho-García and Gosliner (2007) proposed a different interpretation of the diversity of *Paradoris* from eastern and southern Africa.

Discodoris sp. 2 Gosliner, 1987:64, fig. 76.— This is part of *Discodoris cebuensis*.

Discodoris sp. Coleman, 1989:23, unnumbered figure.— This *Discodoris* is the same as the "Milne Bay Discodoris" (Coleman, 2001:56, unnumbered figure). It was found at 20 meters depth, under stones, on reef, in Milne Bay, Papua New Guinea. This animal could hardly be identified without a dissection. It does not look like any of the species dissected here. It could be many things: a *Baptodoris*, a *Geitodoris*, etc.

Peltodoris sp. Perrone, 1990b:24.— The animals (two specimens) were described in seven lines: homogeneously purple-red; dorsal notum not covered by caryophyllidia, and smooth labial cuticle.

Discodoris sp. 1 Behrens, 1991:67.— This is part of *Discodorididae aurila*.

Discodoris sp. 2 Behrens, 1991:67, unnumbered figure.— See *Discodoris* sp. Behrens, 1980.

Peltodoris sp. 1 Behrens, 1991:69.— This is part of *Peltodoris mullineri*.

Discodoris sp. Debelius, 1996:247, unnumbered figure.— This is part of sp. B here.

Discodoris sp. Gosliner, Behrens, and Williams, 1996:159, fig. 558.— This is part of *Hoplodoris estrelyado* Gosliner and Behrens, 1998 (which is now *Carminodoris estrelyado*).

Discodoris sp. Hickman and Finet, 1998:126, unnumbered figure.— This is part of *Hiatodoris* sp. B (see that species described here).

Discodoris sp. 1 Marshall and Willan, 1999:74, fig. 126.— This animal does not seem to be part of any species dissected here. It would remain difficult to propose any identification without a dissection.

Discodoris sp. Masuda, 1999:115, unnumbered figure.— This 30 mm long animal, collected from Kerama Islands, Japan, clearly is part of the species recently described as *Paradoris* sp. B (Dayrat 2006).

Discodoris sp. 1 Ono, 1999:105, fig. 168.— This is part of *Paradoris* sp. B Dayrat, 2006.

Discodoris sp. 2 Ono, 1999:105, fig. 169.— The presence of what seems to be a five-lobed branchial sheath suggests that this 30 mm long animal, collected at 4 meters depth from Zamami Island, Japan, might belong to *Platydoris*.

Discodoris sp. 3 Ono, 1999:106, fig. 170.— This is part of *Discodorididae cebuensis*.

Discodoris sp. 4 Ono, 1999:106, fig. 171.— This 20 mm long animal collected at 5 meters depth from Gahi Island, Japan, does not look like anything examined in the context of this study. It is difficult to guess what it could be without being able to look at the specimen, but the dorsal, roundish tubercles could suggest it might belong to *Paradoris*, although this is tentative.

Discodoris sp. 5 Ono, 1999:107, fig. 172.— My intuition for this 35 mm long animal, collected at 5 meters depth from Zamami Island, Japan, is that it is part of one (likely new) species close to *Discodoris boholiensis* and *Discodoris cebuensis*. My intuition is based on the shape of the fragile, slender gills, and more importantly the larger, white tubercles. However, this is just an intuition.

Discodoris sp. 6 Ono, 1999:107, fig. 173.— This 10 mm long, red-orange animal, collected at 5 meters depth, from Gahi Island, Japan, is too red to be a *Discodoris*! Could it be a *Rostanga*?

Discodoris sp. 7 Ono, 1999:108, fig. 174.— The presence of *Sclerodoris*-like ridges on the dorsal notum of this 7 mm long, creamish animal, collected at 15 meters depth, from Zamami Island, Japan, suggests that it belongs to *Sclerodoris*.

Discodoris sp. 8 Ono, 1999:108, fig. 175.— This 5 mm long animal, collected in the intertidal zone from Zamami Island, Japan, is probably part of *Paradoris* sp. B Dayrat, 2006, although the infra-specific variation of this species is poorly known (see Dayrat 2006 for more information).

Discodoris sp. 9 Ono, 1999:109, fig. 176.— This animal may not belong to *Discodorididae*.

Doridacea sp. A Suzuki, 2000:118, unnumbered figure (also called *Discodoris* in text).— Without an examination and a dissection, it is difficult to determine what this bright yellow, 40 mm long animal (collected from Izu Oceanic Park, at depth 15 m) could be. Could it be *Geitodoris lutea*?

Doridacea sp. B Suzuki, 2000:118, unnumbered figure (also called *Discodoris* in text).— Without an examination and a dissection, it is difficult to determine what this reddish-brown (dorsal tubercles with white apex), 30 mm long animal (collected from Osezaki, Izu Peninsula, at 20 m depth) could be.

Discodoris sp. "blistery Discodoris" Coleman, 2001:56, unnumbered figure.— Coleman rightly points out that this light creamish animal (collected from the North Great Barrier Reef, at 10 meters depth) seems to be undescribed. Without an examination or a dissection, nothing can be written. Depending on the exact shape of the dorsal papillae (there seems to be some papillae that are larger than other ones) then it could be a *Thordisa* or a *Paradoris* (but tentatively).

Discodoris sp. "dappled Discodoris" Coleman, 2001:56, unnumbered figure.— This light pinkish-reddish animal (collected from Portsea, Victoria, Australia, at 10 meters depth) could be one the *Rostanga* species from southern Australia. However, as usual, without an examination or a dissection, it is hard to have an opinion.

Discodoris sp. "maze Discodoris" Coleman, 2001:56, unnumbered figure.— This bright red animal (collected from Ethiburg, South Australia, at 5 meters depth, on a sponge) could also well be a *Rostanga* (because of the bright red color, and the sponge feeding behavior). However, without an examination or a dissection, it is impossible to be positive.

Discodoris sp. "mildewed Discodoris" Coleman, 2001:56, unnumbered figure "AMPI 249."— This is part of *Discodorididae coerulescens*.

Discodoris sp. "Milne Bay Discodoris" Coleman, 2001:56, unnumbered figure.— As Coleman points out, this light creamish-pinkish animal (collected from the Milne Bay, Papua New Guinea, at 20 meters depth) probably is undescribed. The few, white papillae, which are larger than the rest of the tubercles, probably will help: similar papillae can be found in *Discodoris* species, such as *Discodoris cebuensis*, as well as other group such as *Taringa* or *Thordisa* (although all those papillae are actually different). In other words, it is difficult to determine what this animal is without dissecting it.

Discodoris sp. "rosette Discodoris" Coleman, 2001:56, unnumbered figure "AMPI 215."— This animal is part of *Sebadoris fragilis*.

Discodoris sp. "spongy Discodoris" Coleman, 2001:56, unnumbered figure.— This creamish animal (collected from Clovelly [~34° S], New South Wales, Australia, at 10 meters depth, on a sponge) could be (tentatively) a *Paradoris dubia*. If it were to be the case, it would be interesting because Clovelly would probably be the northernmost locality for a species which is primarily found in South Australia, Victoria, and Tasmania. Also, if it were to be correct, the eggs on the picture would be the first picture of the egg mass of *dubia*. However, as always, it is just a hypothesis because it would be necessary to examine the specimen.

Discodoris sp. Valdés, 2001:271-274, figs 2I, 25-26.— This refers to a single specimen that could be part of *Discodorididae achroma* (Valdés, 2001).

Discodoris sp. A Tonozuka 2003:109, unnumbered figure.— This 20 mm long specimen collected from Bali, at 10 meters depth, could be part of *Tayuva lilacina*, but it would have to be dissected to confirm this identification.

Discodoris sp. B Tonozuka 2003:109, unnumbered figure.— This is part of *Paradoris liturata*.

Discodoris sp. 1 Ono, 2004:134-135, fig. 272.— Ono published pictures of four different individuals (all from Ryukyu Islands, southern Japan) that seem to be part of *Paradoris* sp. B Dayrat, 2006. One of the four individuals (#0-670) has a different dorsal pigmentation (it bears brown lines instead of spots): it may or may not be part of *Paradoris* sp. B. The infra-specific variation of this species is poorly known (see Dayrat 2006 for more information).

Discodoris sp. 2 Ono, 2004:136.— Ono published pictures of four different individuals (all from Ryukyu Islands, southern Japan) that are likely part of *cebuensis*. The maximum length is 20 mm. One of the pictures illustrates an interesting color variant with a light dorsal color, which suggests that color variation is higher than what is currently known in that species.

Discodoris sp. Behrens, 2005:25, unnumbered figure.— Berhens published a color picture of an animal identified as *Discodoris* sp., with no description. This animal likely is part of the same species as Coleman's (2001:60) *Jorunna* sp., from Papua New Guinea (called Halstead's *Jorunna* because it was photographed by Bob Halstead). The dorsal color is white (for the background) with large brown blotches (circular in the median area and more elongated on the lateral wing of the dorsal notum). No identification can be proposed without a dissection. It might (very hypothetically) be related to a species such as *Peltodoris mullineri*, with which it shares a similar external appearance (rather flattened body clear background with large blotches).

Discodoris sp. Camacho-Garcia, Gosliner, & Valdés, 2005:86, unnumbered figure.— This is part of *Discodorididae aliciae* Dayrat, 2005.

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Appendix 1

Table of former and current species and subspecies names associated with the genera *Discodoris*, *Peltodoris*, and *Anisodoris*.

Specific name (names currently valid are in bold)	**Authorship**	**Original generic Name**	**Generic name for current ICZN combination (new combination in bold)**	**Clade address for an alternative ICPN combination**	**Previous status**	**Current status (new status in bold)**
achroma	Valdés, 2001	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	Valid
alba	White, 1952	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
aliciae	Dayrat, 2005	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	Valid
amboinensis	Bergh, 1890	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
angulata	Eliot, 1903	*Peltodoris*	***"Doris"***	*Doridina*	Valid	**Nomen dubium**
annuligera	Bergh, 1876	*Kentrodoris*	*Jorunna*	*Jorunna*	Synonym	Synonym (*Jorunna funebris*)
atromaculata	Bergh, 1880	*Peltodoris*	*Peltodoris*	*Peltodoris*	Valid	Valid
aurea	Eliot, 1903	*Peltodoris*	***"Montereina"***	*Discodorididae*	Valid	**Poorly-known species name**
aurila	Marcus and Marcus, 1967	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	Valid
australis	Rudman and Avern, 1989	*Rostanga*	*Rostanga*	*Rostanga*	Valid	**New synonym** (*Rostanga crawfordi*)
boholiensis	Bergh, 1877	*Discodoris*	*Discodoris*	*Discodoris*	Valid	Valid
branneri	MacFarland, 1909	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	Valid
cavernae	Starmühlner, 1955	*Discodoris*	*Paradoris*	*Paradoris*	Synonym	Synonym (*Paradoris indecora*)
cebuensis	Bergh, 1877	*Discodoris*	*Discodoris*	*Discodoris*	Valid	Valid
coerulescens	Bergh, 1888	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	Valid
caerulescens variegata	Eliot, 1903	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
concinna	Alder and Hancock, 1864	*Doris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
concinniformis	Bergh, 1888	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
concinniformis var.	Bergh, 1888	*Discodoris*	***Sebadoris***	*Discodorididae*	Valid	**New synonym** (*Sebadoris fragilis*)
confusa	Ballesteros, Llera and Ortea, 1985	*Discodoris*	***Tayuva***	*Tayuva*	Valid	**New synonym** (*Tayuva lilacina*)
crawfordi	Burn, 1969	*Discodoris*	***Rostanga***	*Rostanga*	Valid	Valid
crosslandi	Eliot, 1903	*Thordisa*	*Sebadoris*	*Sebadoris*	Synonym	Synonym (*Sebadoris nubilosa*)
crucis	Ørsted in Mörch, 186	*Doris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
desmoparypha	Bergh, 1880	*Hoplodoris*	***Asteronotus***	*Asteronotus*	Valid	**New synonym** (*Asteronotus raripilosa*)
dubia	Bergh, 1904	*Discodoris*	*Paradoris*	*Paradoris*	Valid	Valid
edwardsi	Vayssière, 1902	*Discodoris*	***"Doris"***	*Doridina*	Valid	**Poorly-known species name**
egena	Bergh, 1904	*Discodoris*	*Paradoris*	*Paradoris*	Synonym	Synonym (*Paradoris dubia*)
ellioti	Alder and Hancock, 1864	*Doris*	*Platydoris*	*Platydoris*	Valid	Valid
erubescens	Bergh, 1884	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Poorly-known species name**
erythraeensis	Vayssière, 1912	*Discodoris*	*Paradoris*	*Paradoris*	Valid	Valid

Specific name (names currently valid are in bold)	Authorship	Original generic Name	Generic name for current ICZN combination (new combination in bold)	Clade address for an alternative ICPN combination	Previous status	Current status (new status in bold)
evelinae	Marcus 1955	*Discodoris*	**"*Montereina*"**	*Discodorididae*	Valid	**New synonym** (*Discodorididae branneri*)
fellowsi	Kay and Young, 1969	*Peltodoris*	***Hiatodoris***	*Hiatodoris*	Valid	Valid
flindersi	Burn, 1962	*Anisodoris*	**"*Montereina*"**	*Discodorididae*	Valid	**Poorly-known species name**
fragilis	Alder and Hancock, 1864	*Doris*	***Sebadoris***	*Sebadoris*	Valid	Valid
fulva	O'Donoghue, 1924	*Discodoris*	***Geitodoris***	*Geitodoris*	Valid	**New synonym** (*Geitodoris heathi*)
gigantea	Bergh, 1905	*Diaulula*	*Sebadoris*	*Sebadoris*	Synonym	Synonym (*Sebadoris nubilosa*)
golaia	Marcus and Marcus, 1966	*Discodoris*	**"*Montereina*"**	*Discodorididae*	Valid	**Poorly-known species name**
granulata	Ehrenberg, 1831	*Doris*	***Sebadoris***	*Sebadoris*	Valid	**New synonym** (*Sebadoris fragilis*)
greeleyi	MacFarland, 1909	*Peltodoris*	**"*Montereina*"**	*Discodorididae*	Valid	Valid
hawaiiensis	Kay and Young, 1969	*Archidoris*	**"*Montereina*"**	*Discodorididae*	Valid	**New synonym** (*Discodorididae rubra*)
heathi	MacFarland, 1905	*Discodoris*	*Geitodoris*	*Geitodoris*	Valid	Valid
hedgpethi	Marcus and Marcus, 1960	*Discodoris*	**"*Montereina*"**	*Discodorididae*	Synonym	Synonym (*Discodorididae branneri*)
hedleyi	O'Donoghue, 1924	*Alloiodoris*	***Sebadoris***	*Sebadoris*	Valid	**New synonym** (*Sebadoris fragilis*)
hummelincki	Marcus and Marcus, 1963	*Peltodoris*	***Tayuva***	*Tayuva*	Valid	**New synonym** (*Tayuva lilacina*)
hummelincki igla	Marcus and Marcus, 1967	*Peltodoris*	**"*Montereina*"**	*Discodorididae*	Valid	**Nomen dubium**
indecora	Bergh, 1881	*Discodoris*	*Paradoris*	*Paradoris*	Valid	Valid
indicus	O'Donoghue, 1932	*Argus*	*Sebadoris*	*Sebadoris*	Synonym	Synonym (*Sebadoris nubilosa*)
ketos	Marcus and Marcus, 1967	*Tayuva*	*Tayuva*	*Tayuva*	Valid	**New synonym** (*Tayuva lilacina*)
ketos ketos	Marcus and Marcus, 1970	*Tayuva*	*Tayuva*	*Tayuva*	Valid	**New synonym** (*Tayuva lilacina*)
ketos gila	Marcus and Marcus, 1970	*Tayuva*	*Tayuva*	*Tayuva*	Valid	**New synonym** (*Tayuva lilacina*)
ketos juva	Marcus and Marcus, 1970	*Tayuva*	*Tayuva*	*Tayuva*	Valid	**New synonym** (*Tayuva lilacina*)
labifera	Abraham, 1877	*Doris*	**"*Montereina*"**	*Discodorididae*	Valid	Valid
lancei	Millen and Bertsch, 2000	*Peltodoris*	**"*Montereina*"**	*Discodorididae*	Valid	Valid
lentiginosa	Millen, 1982	*Anisodoris*	**"*Montereina*"**	*Discodorididae*	Valid	Valid
lilacina	Gould, 1852	*Doris*	*Tayuva*	*Tayuva*	Valid	Valid
lippa	Valdés, 2001	*Peltodoris*	**"*Montereina*"**	*Discodorididae*	Valid	Valid
liturata	Bergh, 1905	*Discodoris*	*Paradoris*	*Paradoris*	Valid	Valid
lora	Marcus, 1965	*Discodoris*	*Paradoris*	*Paradoris*	Nomen dubium	Nomen dubium

Specific name (names currently valid are in bold)	Authorship	Original generic Name	Generic name for current ICZN combination (new combination in bold)	Clade address for an alternative ICPN combination	Previous status	Current status (new status in bold)
lutescens	Bergh, 1905	*Discodoris*	*Rostanga*	*Rostanga*	Valid	Valid
maculosa	Cuvier, 1804	*Doris*	"*Doris*"	*Doridina*	Synonym	**Nomen dubium**
maculosa	Bergh, 1884	*Discodoris*	*Tayuva*	*Tayuva*	Valid	**New synonym** (*Tayuva lilacina*)
mauritiana	Bergh, 1889	*Peltodoris*	*Peltodoris*	*Peltodoris*	Valid	**New synonym** (*Peltodoris murrea*)
mavis	Marcus and Marcus, 1967	*Discodoris*	*Geitodoris*	*Geitodoris*	Valid	Valid
meta	Bergh, 1877	*Discodoris*	*Discodoris*	*Discodoris*	Synonym	Synonym (*Discodoris boholiensis*)
millegrana	Alder and Hancock, 1854	*Doris*	*Aporodoris*	*Aporodoris*	Valid	**Poorly-known species name**
modesta	Bergh, 1877	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
morphaea	Bergh, 1877	*Discodoris*	***Sebadoris***	*Sebadoris*	Synonym	Synonym (*Sebadoris fragilis*)
mortenseni	Marcus and Marcus, 1963	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	Valid
mullineri	Millen and Bertsch, 2000	*Peltodoris*	*Peltodoris*	*Peltodoris*	Valid	Valid
murrea	Abraham, 1877	*Doris*	***Peltodoris***	*Peltodoris*	Valid	Valid
muta	Bergh, 1877	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
nayarita	Ortea and Llera, 1981	*Peltodoris*	***"Montereina"***	*Discodorididae*	Synonym	Synonym (*Discodorid-idae greeleyi*)
nobilis	MacFarland, 1905	*Montereina*	***"Montereina"***	*Discodorididae*	Valid	Valid
notha	Bergh, 1877	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
notiperda	Risbec, 1956	*Discodoris*	***Sebadoris***	*Sebadoris*	Valid	**New synonym** (*Sebadoris fragilis*)
noumeae	Risbec, 1937	*Peltodoris*	***"Doris"***	*Doridina*	Valid	**Nomen dubium**
nubilosa	Pease, 1871	*Doris*	*Sebadoris*	*Sebadoris*	Valid	Valid
opisthidia	Bergh, 1877	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
orbignyi	H. and A. Adams, 1858	*Doris*	N/A	N/A	Permnent-ly invalid	Permanently invalid
pallida	Baba, 1937	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Poorly-known species name**
palma	Allan, 1933	*Discodoris*	***Tayuva***	*Tayuva*	Valid	**New synonym** (*Tayuva lilacina*)
papillata	Eliot, 1903	*Platydoris*	***Asteronotus***	*Asteronotus*	Valid	**New synonym** (*Asteronotus raripilosa*)
pardalis	Alder and Hancock, 1864	*Doris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
paroa	Burn, 1969	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Poorly-known species name**
patriziae	Perrone, 1991	*Discodoris*	***"Doris"***	*Doridina*	Valid	**Nomen dubium**
phoca	Marcus and Marcus, 1967	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Poorly-known species name**
planata	Alder and Hancock, 1846	*Doris*	*Geitodoris*	*Geitodoris*	Valid	Valid
prea	Marcus and Marcus, 1967	*Anisodoris*	***"Doris"***	*Doridina*	Valid	**Poorly-known species name**

Specific name (names currently valid are in bold)	**Authorship**	**Original generic Name**	**Generic name for current ICZN combination (new combination in bold)**	**Clade address for an alternative ICPN combination**	**Previous status**	**Current status (new status in bold)**
punctata	d'Orbigny, 1839	*Doris*	N/A	N/A	Permanently invalid	Permanently invalid
punctifera	Abraham, 1877	*Doris*	***"Montereina"***	*Discodorididae*	Valid	**Poorly-known species name**
punctuolata	d'Orbigny, 1837	*Doris*	***"Montereina"***	*Discodorididae*	Valid	Valid
purcina	Marcus and Marcus, 1967	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Poorly-known species name**
pusae	Marcus, 1955	*Discodoris*	*Geitodoris*	*Geitodoris*	Valid	Valid
raripilosa	Abraham, 1877	*Doris*	***Asteronotus***	*Asteronotus*	Valid	Valid
rosi	Ortea, 1979	*Discodoris*	*Rostanga*	*Rostanga*	Valid	Valid
rubens	Vayssière, 1919	*Discodoris*	***Geitodoris***	*Geitodoris*	Valid	**Nomen dubium**
rubescens	Bergh, 1905	*Peltodoris*	***"Doris"***	*Doridina*	Valid	**Poorly-known species name**
rubra	Bergh, 1905	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	Valid
sandiegensis	Cooper, 1863	*Doris*	***"Montereina"***	*Discodorididae*	Valid	Valid
sauvagei	Rochebrune, 1881	*Peltodoris*	***"Montereina"***	*Discodorididae*	Valid	**Poorly-known species name**
schmeltziana	Garrett in Bergh, 1875	*Discodoris*	*"Doris"*	*Doridina*	Valid	**Nomen dubium**
sibogae	Bergh, 1905	*Anisodoris*	***"Montereina"***	*Discodorididae*	Valid	**Poorly-known species name**
sibogae	Bergh, 1905	*Discodoris*	*Platydoris*	*Platydoris*	Synonym	Synonym (*Platydoris scabra*)
sordida	Quoy and Gaimard, 1832	*Doris*	N/A	N/A	Permanently invalid	Permanently invalid
sordidata	Abraham, 1877	*Doris*	***Sebadoris***	*Sebadoris*	Valid	**New synonym** (*Sebadoris fragilis*)
sordii	Perrone, 1990	*Peltodoris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
spetteda	Marcus and Marcus, 1966	*Discodoris*	N/A	N/A	Nomen nudum	Nomen nudum
stellifera	Vayssière, 1903	*Archidoris*	***"Doris"***	*Doridina*	Valid	**Poorly-known species name**
stragulata	Abraham, 1877	*Doris*	***Sebadoris***	*Sebadoris*	Valid	**New synonym** (*Sebadoris fragilis*)
testudinaria	Risso, 1818	*Doris*	*"Doris"*	*Doridina*	Nomen dubium	Nomen dubium
tema	Edmunds, 1968	*Discodoris*	*Geitodoris*	*Geitodoris*	Valid	Valid
timorensis	Bergh, 1905	*Anisodoris*	***"Doris"***	*Doridina*	Valid	**Nomen dubium**
tristis	Bergh, 1899	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**
turia	Burn, 1969	*Discodoris*	***Rostanga***	*Rostanga*	Valid	**New synonym** (*Rostanga crawfordi*)
vanikoro	Pruvot-Fol, 1934	*Discodoris*	***Sebadoris***	*Sebadoris*	Valid	**New synonym** (*Sebadoris fragilis*)
versicolor	Bergh, 1905	*Discodoris*	***"Doris"***	*Doridina*	Valid	**Nomen dubium**
vestita	Abraham, 1877	*Doris*	***"Montereina"***	*Discodorididae*	Synonym	Synonym (*Discodorididae punctuolata*)
voniheringi	MacFarland, 1909	*Discodoris*	***"Montereina"***	*Discodorididae*	Valid	**Nomen dubium**

Specific name (names currently valid are in bold)	**Authorship**	**Original generic Name**	**Generic name for current ICZN combination (new combination in bold)**	**Clade address for an alternative ICPN combination**	**Previous status**	**Current status (new status in bold)**
whitleyi	Allan, 1932	*Discodoris*	***Jorunna***	*Jorunna*	Valid	**New synonym** (*Jorunna funebris*)
winckworthi	White, 1948	*Otinodoris*	***Asteronotus***	*Asteronotus*	Valid	**New synonym** (*Asteronotus raripilosa*)
worki	Marcus and Marcus, 1967	*Anisodoris*	**"*Montereina*"**	*Discodorididae*	Valid	Valid
ylva	Marcus, 1965		**"*Montereina*"**	*Discodorididae*	Valid	**Poorly-known species name**
yaeyamensis	Baba, 1936	*Discodoris*	**"*Montereina*"**	*Discodorididae*	Valid	**Nomen dubium**
ylva	Marcus, 1965	*Discodoris*	**"*Montereina*"**	*Discodorididae*	Valid	**Poorly-known species name**
zibethina	Bergh, 1878	*Fracassa*	**"*Montereina*"**	*Discodorididae*	Valid	**Nomen dubium**

Appendix 2

List of SEM preparations for the radula, labial cuticle, dorsal notum, penis, rhinophores, branchial plumes, muscular wall (mw) in the distal part of the reproductive system, dorsal ganglia of the central nervous system (ns), the oral tentacles (ot), and the spine of the accessory gland (as). The last four organs are listed in the column "Others." Letters indicate: organs that were missing ("M") because of dissection prior to the present study; organs lost ("L") during its preparation (most often after critical point drying); organs preserved on a slide ("S") prepared by previous workers; organs absent ("A"), usually the penis, although the specimen did not seem immature sexually; and finally, organs absent (usually the penis) because the specimen was sexually immature ("I"). Parentheses indicate that the organ prepared could belong to any specimen in the lot (because the organs were found mixed all together within the same jar with several specimens in it). Only the specimens for which I prepared some SEM stubs are mentioned in this table.

Museum Lot	Locality	Spm #	Size (mm)	Rad.	Lab. Cut.	Not.	Pen.	Rhi.	BP.	Others
atromaculata										
MNCN 1.984	Spain		20/12	x					x	
MNCN 18240		1	60/50	x		x		x	x	
		2	36/22	x				x	x	
MNCN 18242			60/40	x						
MNCN 18243		1	55/40	x		x				
		2	50/40	x						
MNCN 19.326	Mallorca		45/35	x		x	x			
MNCN 19.336			50/35	x	x					
MNCN 46485	Portugal		35/25	x	x	x				
CASIZ 072584	Azores		50/40	x		x			x	
aurila										
Syntype	Panama	1	20/10		x					
		2	15/12			x				
CASIZ 159788	Costa Rica		9/5	x	x					
CASIZ 072900	Baja California		27/17	x	x	x			x	
CASIZ 072898		1	28/22	x	x	x		x	x	
		2	28/18	x	x					
		3	25/16	x	x	x		x		
		4	25/16	M	M	x				
CASIZ 072897			17/10	x	x	x				
CASIZ 122177		1	7/12	x	x					
		2	8/6	x	x					
		3	9/6	x	x					
		4	7/5	x	x	x		x		
boholiensis										
Syntype	Philippines		70/40			x				
CASIZ 073543	Madagascar		8/4	x	x					
NMV F86409	Australia (NT)		60/40	x	x	x				
AM C148492			16/14	x	x					
AM C144581	Coral Sea		20/8	x	x					
CASIZ 087129	Indonesia		14/8			x		x	x	
CASIZ 073520	PNG		20/15	x	x				x	
CASIZ 113654			35/20	x	x				x	
CASIZ 158768	Philippines	1	45/25	x	x	x		x	x	
		2	40/20	x	x					
CASIZ 071277			18/15	x	x			x	x	
AM C104084			70/50	x	?					

Museum Lot	Locality	Spm #	Size (mm)	Rad.	Lab. Cut.	Not.	Pen.	Rhi.	BP.	Others
CASIZ 070225	Japan		20/10	x	x			x		
branneri										
Holot. *branneri*	Brazil		29/15	S	S	x				
Paralect. *crucis*	Virgin Isl.	3	53/25	x	x	x	x	x		
Synt. *hedgpethi*	Texas	1	40/25	M	M		(x)			
		2	36/24	M	M		(x)			
		3	29/13	M	M		(x)			
Paralect. *notha*	Guadeloupe	1	45/27	M	M		x			
		2	36/27	x	x	x	x			
NMNH 576292	Florida		56/40	S	S	x	S			
CASIZ 072292	Bahamas	1	45/30	x	x	L	x	x	x	
		2	38/25	x	x	x	x			
		2	43/27	M	M	x			x	
		3	40/20	S	M	x				
CASIZ 010571	Panama		27/25	S	M	x	x			
CASIZ 010572		1	60/35	S	M	x	x			
		2	26/15	M	M		x			
CASIZ 010580			29/20	S	M	x	x			
MCZ 288294	Brazil	1	35/20	x	x	x	x			
		2	30/15	x	x		x			
MZSP 37929		1	55/35	M	M		x			
		2	53/30				x	x		
		3	36/25				x			
cebuensis										
Holot. *cebuensis*	Philippines		26/17	M	M	x				
CASIZ 110381			57/38	x	x	x		x		
CASIZ 110447			37/25	x		x		x	x	
CASIZ 156672			27/18	x	x			x	x	
CASIZ 106482			20/8	x				L		
CASIZ 093937	Indonesia		27/24	x						
CASIZ 070018	Japan		55/35	x	x	x		x		
CASIZ 070019			85/55	x	x			x		
CASIZ 168013	Hawaii		25/15	x				L		
coerulescens										
CASIZ 161292	Madagascar		11/4	x	x					
CASIZ 074198	Seychelles		23/12	x	x	x	A	x	x	
CASIZ 086325	PNG		15/7	x	x	x	x		x	
CASIZ 103713	Philippines		25/13	x	x	x	x	x	x	

Museum Lot	Locality	Spm #	Size (mm)	Rad.	Lab. Cut.	Not.	Pen.	Rhi.	BP.	Others
CASIZ 105689			15/6	x	x		x		x	
CASIZ 157476			17/8	x	L		x			
CASIZ 070167	Japan		20/12	x	x	x				
MNHN	New Caled.	1	24/15	x	x	x	x	x	x	
		2	15/9	x			x			
CASIZ 071702	Cook Islands		20/15	x	x	x	x			
crawfordi										
Holotype	Western Austr.		21/14	x	M		M			
Paratype		1	16/9	x	x	x	x			
Paratype		2	13/7	x	M		M			
NMV F86412	Victoria		18/12	x	x	x	A	x		
NMV F30607			21/15			x			x	
NMV F86411			15/11	x	x	x	x	x		
crucis										
Lectotype	Virgin Is.		50/30	x		x				
Paralect. (#2)			53/35	x		x				
fellowsi										
Paratype	Hawaii		34/24	x	x	x				
CASIZ 166765			25/17	x	x	x	x			
fragilis										
Lectot. *notiperda*	Vietnam		55/30	x	x	x	x			
CASIZ 170083	Red Sea		35/20	x			x			
MNHN	Djibouti	1	80/50	x	x	x	x	x	x	
CASIZ 099383	Tanzania		65/50	x	x	x	x			
CASIZ 073234	Madagascar	1	80/60	x		x		x	x	
		2	80/50	x			x			
		3	50/25	x	x		x			
CASIZ 168931			40/17	x			x			
CASIZ 074201	Seychelles		70/55	x	x	x	M	x	x	
CASIZ 074075			35/25	x			x			
CASIZ 074248		1	40/30	x	x	x	x			
		2	40/25	M	M		M			
CASIZ 074193		1	50/35	x			x			
		2	50/30	x	x	x	x			
		3	50/30	x	x	x	L			
		4	50/30	x			x			
		5	40/25	x						

Museum Lot	Locality	Spm #	Size (mm)	Rad.	Lab. Cut.	Not.	Pen.	Rhi.	BP.	Others
CASIZ 144022	Western Austr.		55/50	M	M		x			
CASIZ 144007			60/40				M			
AM C418411		1	60/45	x			x			
		2	35/20	x			A			
AM C126086	NSW		90/50				x			
AM C415874			60/40	x	x	x	x			
AM C164559			65/40				x			
AM C418345		1	80/60	x						
		2	50/45				x			
AM C133000			60/55				x			
AM C153601	North. Terr.		80/50	x			x			
AM C418417	Queensland		70/40	x	x	x	x			
NMV F79395			45/35				x			
AM C415872		1	80/50				x			
		3	65/40	x	x	x	x			
AM C147842			70/55				x			
AM C418416		1	70/40				x			
		3	35/20	x			A			
AM C418412			75/45				x			
AM C418348			65/40				x			
AM C099293			55/35				x			
AM C418309		2	45/35				x			
AM C125915		1	70/45	x			L			
		2	70/45				x			
AM C416540		1	65/35				x			
		2	40/20				x			
AM C416545			35/25	x	x		A			
NMV F86414		1	90/55	x			x	x		
		2	80/60				x			
MCZ 048029	Fiji		65/50				x			
MNHN	New Caled.		25/13							
MNHN (1252)		1	85/60				x			
		2	65/40	x	x	x	x	x	x	
		3	60/40				x	x		
		4	60/40				x			
		5	55/35				x			
		8	18/14	x	x		A	x		

Museum Lot	**Locality**	**Spm #**	**Size**	**Rad.**	**Lab.**	**Not.**	**Pen.**	**Rhi.**	**BP.**	**Others**
			(mm)		**Cut.**					
USNM 577550	Thailand	1	70/50	x			x			
		2	25/16				x			
		4	15/10	x			A			
		6	10/7	x			A	x		
ZMUC	Indonesia		45/20				x			
CASIZ 096306	Philippines		95/55	x			x			
CASIZ 070011	Japan		65/45	x	x	x	x			
CASIZ 074590	Samoa		55/45	x	x		x			
CASIZ 121231	Marshall		40/30	x			M			
CASIZ 121232		2	65/35	x	x	x	x			
CASIZ 121234			45/30	x	M		M			
golaia										
Holotype	Gulf Guinea		38/26	S	S	x				
greeleyi										
Holotype	Brazil		18/10			x				
MCZ 288303		1	7/4	x	x					
MCZ 288303		2	6/4			x		x	x	
igla										
Holotype						x				
labifera										
Syntype	Seychelles		26/15	x	x	x	x			
lancei										
Holotype	Gulf California		55/45			x				
Parat. (118572)			60/50			x				
lilacina	**Caribbean**									
Par. *hummelincki*			45/35	x	x	x	x	x		
Paral. #4 *crucis*	Virgin Isl.		60/35	x			x			
CASIZ 077318	Cayman Isl.	1	20/10	x	x	x	x	x	x	
		2	20/10	x						
lilacina	**East. Pacific**									
CASIZ 078386	Galapagos		22/14	x	x	x	x			
CASIZ 088214	Panama		10/6	x	x	x	x	x		
NMNH 739594			12/10	x	x		x			
CASIZ 088239			37/25	x	x	x	x		x	
CASIZ 088251			29/17	x	x		x	x	x	
CASIZ 069113	Mexico	1	36/20	x	x	x	x	x	x	mw
		2	25/17				x			

Museum Lot	Locality	Spm #	Size (mm)	Rad.	Lab. Cut.	Not.	Pen.	Rhi.	BP.	Others
CASIZ 069108		1	35/22	x		x	x			
		2	25/20	x			x			mw
		3	25/20	x			x			
		4	25/20	x			x			
CASIZ 001569		1	40/25	x			x			
		2	35/20	x			x			
CASIZ 157399			35/25	x	x		x			
CASIZ 081808			40/30	x		x	x			
CASIZ 074630		2	35/20	x	x	x	x			
CASIZ 004291		1	45/30	x	x		x			
		2	40/25	x			L			
CASIZ 073165			35/20	x	x	x	x	x	x	
USNM 753638			26/11	M		x	M	x		
CASIZ 071415			23/15	x						
lilacina	**IW Pacific**									
CASIZ 073468	South Africa		30/20	x	x	x	x	x		
CASIZ 099332	Tanzania		30/15	x	x	x	x			
CASIZ 073241	Madagascar		15/10	x	L	x	L			mw
AM C418422	Lord Howe Isl.		30/20				x			
AM C132317			30/22	x	x		x			
AM C418420			25/25	x			x			
AM C115270	NSW	1	42/25	x	x			x		
AM C142251		1	20/12	x	x		x			
		2	20/12				x			
AM C123599			40/30	x	x		x			
AM C113759			40/20				x			
AM C126481			40/25			x	x		x	
AM C125186			20/10	x	x	x	L	x	x	
AM C132958		1	15/9	x	x	x	x		x	
		2	15/9				x		x	
		5	9/6	x	x		I	x	x	
AM C155707		1	19/12				x			
NMV F86423			22/15	x	x	x	x			
NMV F86422			22/14	x	x	x	x			
AM C132978		1	15/9			x	x			
		2	13/7				x		x	
CASIZ 068283	Indonesia		20/13	x	x	x	x			

Museum Lot	**Locality**	**Spm #**	**Size**	**Rad.**	**Lab.**	**Not.**	**Pen.**	**Rhi.**	**BP.**	**Others**
			(mm)		**Cut.**					
CASIZ 065363	PNG		18/10	x	x	x	x	x	x	
CASIZ 068753			11/7	L	L	x	L	x	x	
			10/6		x					
CASIZ 065365			12/6	x	x	x	x	x	x	
CASIZ 071610			10/5	x	x					
CASIZ 072829			15/10	x	x		L			
CASIZ 072830			8/6	x	L		x			
CASIZ 086307		1	10/7	x		x	x	x	x	
CASIZ 156947	Philippines		14/8	x	x	x	x			
CASIZ 158266		1	30/17	x	x	x	x	x	x	
CASIZ 103770			18/10	x	x	x	x			mw
CASIZ 157146			12/7							
CASIZ 168913	Marshall		50/35	x	x	x		x		
CASIZ 168914			45/30	x	x					
CASIZ 069969	Japan		30/17	x	L	x	x			
CASIZ 031862	Hawaii		30/17	x	x	x	x			
CASIZ 061455		1	58/38	x	x		M			
		2	28/15	x	M	x	x			
		3	25/15	M	M	x	M			
CASIZ 071572			40/25	x	x	x	x			
CASIZ 086958			25/13	x	x	x	x			
***lilacina* uncert.**										
CASIZ 073266	Madagascar		8/4	x	x		I			
***lilacina* probl.**										
CASIZ 069742	PNG	1	20/10	x	x	x	x	x	x	
		2	15/8				x			
		3	14/9	x	x	x	x	x	x	
CASIZ 086307		2	9/6	x	x	x	x		x	
		3	8/5				x			
CASIZ 083744	Philippines		28/15	x	x	x	A			
CASIZ 096341			15/8	x	x	x	L			
CASIZ 083651			10/5				x			
lilacina	**Med. East.Atl.**									
Holot. *maculosa*	Naples		30/19			x				
MNCN (801)	Spain		30/17	x	x	x	L			mw
MNCN (769)			38/28	x		x	x			
MNCN (867)			24/16	x			I			

Museum Lot	Locality	Spm #	Size (mm)	Rad.	Lab. Cut.	Not.	Pen.	Rhi.	BP.	Others
LACM 152717	Lebanon		23/12	M	M		x			
ZMUC	Canary Islands		37/23	x		x	x			
lutescens										
CASIZ 109725	Palau		13/7	x	x	x		x	x	
mortenseni										
Holotype	Curaçao		12/9			x				
Paratype	Tobago		9/7			x				
CASIZ 074656	Yucatan	1	10/4	M			M			
		2	9/4	x		x	A	x		
CASIZ 077292	Cayman Isl.	1	24/13	x	x	x	x	x		
		2	19/10	M	M					
		3	14/8	x		x	x		x	
		4	11/7			x	A			
		5	10/6	x			x	x		
NMNH 820894	Belize		10/7	M	M					
CASIZ 074398	Florida Keys		9/4			x	M			
mullineri										
Holotype	California		35/25							
Parat. (069302)			45/35			x				
Parat. (074651)			40/35			x	x			
murrea										
CASIZ 073317	Madagascar		19/7	x	x		x			
CASIZ 070389	Reunion		60/32	x	x	x	x	x	x	
AM C133485	Cocos Islands	1	30/24	x	x		x			
		2	14/10	x			x			
CASIZ 073508	Thailand		26/22	x	x			x		
AM C144547	Queensland		25/17	x	x		A			
AM C107821			25/17	x	x		x			
NVM F80593			30/22	x			x			
MNHN	New Caled.	1	38/22	x	x	x	x	x	x	
		2	32/18	x	x		x	x	x	
CASIZ 079243	Japan		37/17	x	x	x	x			
CASIZ 079249			26/17				x			
muta										
Syntype	Guadeloupe	2	22/15	x	x	x	x			
nobilis										
CASIZ 007098	California	1	45/30	x		x				

Museum Lot	Locality	Spm #	Size	Rad.	Lab.	Not.	Pen.	Rhi.	BP.	Others
			(mm)		Cut.					
		2	40/35			x				
		3	28/17							
CASIZ 087212			20/17			x				
nubilosa										
CASIZ 074202	Seychelles		70/45	x	x	x	x	x		
CASIZ 074254			80/45	x	x	x	x	x	x	
CASIZ 070352	Madagascar	1	65/55	x	x	x	x	x		
NMNH 576413	Hawaii	1	130/90	x			x	x	x	
		2	110/90	x	x		x			
NMNH 576435	Rurutu	1	60/50	x			x			
		2	40/30	x			x			
CASIZ 071727			85/60	M	x		M			
paroa										
Holotype	Victoria		16/7	x						
NMV F96224			8/5	x	x	x				
phoca										
Holotype	Florida		50/30	S	S	x				
punctuolata										
CASIZ 118012	Chile					x				
raripilosa										
CASIZ 073238	Madagascar		155/90	M			M			as, ot
CASIZ 099347	Tanzania		65/55	x	x					as
MCZ 004575	Mauritius		85/55	x						as
NMV F16748	Queensland		80/55	x	x		x			as
CASIZ 109748	PNG	1	65/45	x		x	x			as
		2	75/45	x						ot
		3	45/25	x				x	x	as, ns
ZMUC	Philippines		100/65	x	x		x			as
CASIZ 070066	Japan		80/65	x		x	x	x		as
rosi										
MNCN 1972	Spain		9/5	x		x				
CASIZ 166874	Portugal	1	9/5	x		x				
rubra										
AM C124327	Queensland		110/70	x		x	x	x		
CASIZ 071238	PNG	1	60/37	x		x	x	x	x	
		2	30/20	x	x		x	x		
CASIZ 065782			33/18	x	x	x	x		x	

Museum Lot	Locality	Spm #	Size (mm)	Rad.	Lab. Cut.	Not.	Pen.	Rhi.	BP.	Others
CASIZ 086684	Indonesia		35/22	x	x		x			
CASIZ 081904	Thailand		58/28	x	x		x			
CASIZ 087907	Japan		68/32	x	x	x	x			
Par. *hawaiiensis*	Hawaii		21/17	x	x	x	x	x		
worki										
NMNH 836766	Florida		35/23	x	x	x	x			as
ylva										
Holotype	Gilbert Island		11	M	M	x				
Sp. A										
CASIZ 089040	Okinawa	/9	23/15	x	x	x			x	
Sp. B										
CASIZ 088588	Galapagos		35/25	M	M			x		
CASIZ 097537	Galapagos		17/10	x	x	x				
Sp. C										
CASIZ 082038	Japan		65/55	x	M	x	x	x		
Sp. D										
CASIZ 097534	Galapagos	2	13/7	x		x				
		3	8/5	x	x	x				
		4	4/2	x						
CASIZ 097574	Galapagos	1	14/7	x	x	x	x	x		
		2	12/6			x	x			
		3	11/5			x	x	x		
		4	10/5	x	x		A	x		
		5	10/5	x	x		x	x		
		6	9/5			x	x			
Sp. E										
CASIZ 071657	Gulf Califor.	1	17/10	x	x	x		x		
		2	13/8			x				
		3	9/6	x		x		x		
CASIZ 071810		1	16/7	x	x	x		x	x	
		2	10/5	x						
CASIZ 072928			7/4	x		x		x	x	
CASIZ 072932		1	10/5	x		x				
CASIZ 071871		1	14/10	x	x	x		x	x	
Sp. F										
CASIZ 156663	Philippines		30/15	x	x	x	x	x	x	
Sp. G										

Appendix 3

Data matrix used for cladistic analyses.

Characters	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
Taxa										**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Outgroups																		
verrucosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
antillensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
luteomarginata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
evelinae	0	0/1	0/1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
macfarlandi	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
marcusi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
pseudoargus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
kerguelenensis	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ingroup																		
achroma	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
aliciae	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
atromaculata	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
aurila	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
boholiensis	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1
branneri	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
cebuensis	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
coerulescens	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
crawfordi	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
dubia	1	1	1	0	1	0	0	0	1	0	2	1	0	1	0	0	0	0
*elliot*i	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
erythraeensis	1	1	1	0	1	0	0	0	1	0	2	1	0	1	0	0	0	0
fellowsi	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
fragilis	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
greeleyi	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
heathi	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
indecora	1	1	1	0	1	0	0	0	1	0	2	1	0	1	0	0	0	0
labifera	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
lancei	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
lentiginosa	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
lilacina Indo-West Pac.	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
lilacina East. Pacific	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
lilacina Caribbean	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
lilacina Med. & E. Atl.	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
lippa	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
liturata	1	1	1	1	0	0	0	0	1	0	2	1	0	1	0	0	0	0
lutescens	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0

Characters	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
Taxa										**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Ingroup																		
mavis	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
mortenseni	1	1	0	0	0	0	0/1	0	0	0	1	0	0	0	0	0	0	0
mullineri	1	1	0	0	0	0	0/1	0	0	0	0	0	0	0	0	1	0	0
murrea	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
nobilis	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
nubilosa	1	1	0	0	0	0	0	0	0	0&1	0	0	0	0	0	0	0	0
planata	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
pusae	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
raripilosa	1	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0
rosi	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
rubra	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
sandiegensis	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
worki	1	1	0	0	0/2	0	0	0	0	0	0	0	0	0	0	0	0	0
Nomina dubia																		
alba	1	1	0	0	0	0	?	0	0	0	1	?	?	?	?	?	?	?
amboinensis	1	1	?	0	0	0	?	?	?	?	1	?	?	?	?	0	0	?
angulata	?	?	?	0	?	0	?	0	?	?	0	?	?	?	?	?	?	?
coerulescens v.	1	1	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
concinna	1	1	?	0	0	?	?	0	?	?	1	?	?	?	?	?	?	?
concinniformis	1	1	?	0	0	?	?	0	?	?	1	?	?	?	?	0	?	?
crucis	1	1	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0	?
granulata	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
igla	1	1	0	0	0	0	0	0	?	0	0	?	?	?	?	?	?	?
lora	1	1	1	0	1	0	0	0	1	0	2	1	0	1	0	0	0	0
maculosa Cuv.	?	?	?	0/1	?	?	?	0	?	?	?	?	?	?	?	?	?	?
modesta	1	1	0	0	0	0	0	0	?	0	1	?	?	?	?	0	?	?
muta	1	1	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0
notha	1	1	0	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?
noumeae	0/1	0/1	?	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?
opisthidia	1	1	0	0	0	0	0/1	0	0	0	1	?	?	?	?	?	?	?
pardalis	1	?	?	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?
patriziae	0/1	1	?	0	?	?	0/1	0	?	?	1	?	?	?	?	?	?	?
rubens	1	1	0	0	0	0	?	0	?	?	1	?	?	?	?	0	0	?
schmeltziana	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?
sordii	0/1	1	?	0	?	?	0/1	0	?	?	0	?	?	?	?	?	?	?
testudinaria	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Characters	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
Taxa										**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Nomina dubia																		
timorensis	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?
tristis	1	1	1	?	0	0	0/1	0/1	?	?	1	?	?	?	?	?	?	?
versicolor	0	0	0	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?
voniheringi	1	1	0	0	0	0	0/1	0	?	?	1/2	0	0	0	0	0	0	0
yaeyamensis	1	1	?	0	0	0	?	?	?	?	1	?	?	?	?	?	?	?
zibethina	1	1	0	0	0	0	0	0	0	0	1	?	?	?	?	0	0	0
Poorly known																		
aurea	1	?	?	?	?	?	?	0	?	?	0	?	?	?	?	?	?	?
edwardsi	?	?	?	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?
erubescens	1	1	?	0	0	?	?	?	?	?	1	?	?	?	?	?	?	?
flindersi	1	1	0	0	0/1	0	0	0	0	0	0	?	?	?	?	?	?	?
golaia	1	1	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0
millegrana	1	1	0	0	0	0	0/1	0	?	?	0	0	0	0	0	0	0	0
pallida	1	1	?	0	0	?	?	?	?	?	1	?	?	?	?	0	?	0
paroa	1	1	0	0	?	0	?	0	0	0	1	0	0	0	0	0	0	0
phoca	1	1	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0
prea	0	0	0	0	0&2	0/2	0	0	0	0	0	0	0	0	0	0	0	0
punctifera	1	1	0	0/1	0	0	0/1	0	?	?	0	?	?	?	?	0	0	0
purcina	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
rubescens	?	?	?	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?
sauvagei	1	1	0	0	0	0	0	0	0	?	0	?	?	?	?	0	0	0
sibogae (A)	1	1	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?
stellifera	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
ylva	1	1	0	0	0	?	?	0	0	?	1	?	?	?	?	?	?	?
New species																		
Sp. A	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Sp. B	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sp. C	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Sp. D	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Sp. E	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sp. F	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sp. G	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Other ingroups																		
punctuolata	1	1	0	0	0	0	1	0	0	?	0	0	0	0	0	0	0	0
caespitosus	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
bimaculata	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0

Characters	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
Taxa										**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Other ingroups	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
grandiflora	1	1	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0
estrelyado	1	1	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0
capensis	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
complanata	1	1	0	0	0	0	0	0	1	0	1	0	?	?	?	0	0	0
araneosa	1	1	1	0	1	0	0	0	1	0	?	1	0	1	0	0	0	0
aivica	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
fanabensis	1	1	0	0	0	0	1	0	0	?	0	?	0	0	0	0	0	0
argo	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
tomentosa	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
pardus	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
arbutus	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
pulchra	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Characters	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	
Taxa	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	
Outgroups																		
verrucosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
antillensis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
luteomarginata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
evelinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
macfarlandi	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
marcusi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
pseudoargus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
kerguelenensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ingroup																		
achroma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
aliciae	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	
atromaculata	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	
aurila	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	
boholiensis	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	
branneri	0	0	0	0	0	0	0&1	0	0	0	0	0	2	0	0	0	1	
cebuensis	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	
coerulescens	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	
crawfordi	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
dubia	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	
elliotti	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	1	
erythraeensis	0	1/2	0	0	0	0	0	0	1	0	0	1	2	0	0	0	1	

Characters	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**
Taxa	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**
Ingroup																	
fellowsi	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
fragilis	0	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	1
greeleyi	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
heathi	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	1
indecora	0	1	0	0	0	0	0	0	1	0	0	1	2	0	0	0	1
labifera	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
lancei	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
lentiginosa	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
lilacina Indo-West Pac.	0	0	0	0	0	0	0	1	0	0	0	0	2&3	1	0	0	1
lilacina East. Pacific	0	0	0	0	0	0	0	1	0	0	0	0	2&3	1	0	0	1
lilacina Caribbean	0	0	0	0	0	0	0	1	0	0	0	0	2&3	1	0	0	1
lilacina Med. & E. Atl.	0	0	0	0	0	0	0	1	0	0	0	0	3	1	0	0	1
lippa	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
liturata	0	2	0	0	0	0	0	0	0	0	0	1	2	0	0	0	1
lutescens	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
mavis	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	1
mortenseni	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
mullineri	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
murrea	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
nobilis	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
nubilosa	0	0	0	0	0	1	1	0	0	0	0	0	2	0&1	0	0	1
planata	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	1
pusae	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	1
raripilosa	0	0	0	0	0&1	0	0	0	0	1	0	0	2	0	0	0	1
rosi	1	0	0	0	0	0	0	0	0/1	0	0	0	2	0	0	0	1
rubra	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
sandiegensis	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
worki	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	1
Nomina dubia																	
alba	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
amboinensis	0	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?
angulata	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
coerulescens v.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
concinna	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
concinniformis	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
crucis	0	0	0	0	0	?	?	0	?	?	?	?	?	?	?	?	?

Characters	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**
Taxa	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**
Nomina dubia																	
granulata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
igla	0	?	0	0	?	?	?	?	0	0	0	0	2	0	0	?	?
lora	0	1	0	0	0	?	?	0	?	0	0	?	2	0	0	?	?
maculosa Cuv.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
modesta	0	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?
muta	0	0	0	0	0	0	0	0/1	0	0	0	0	2	0/1	0	0	1
notha	0	?	0	0	0	?	0	0/1	0	0	0	0	2	?	?	?	?
noumeae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nomina dubia																	
opisthidia	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
pardalis	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
patriziae	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
rubens	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?
schmeltziana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
sordii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
testudinaria	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
timorensis	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
tristis	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
versicolor	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
voniheringi	0	0	0	0	0	?	?	0	0	0	0	0	2	0	0	0	1
yaeyamensis	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
zibethina	0	0	0	0	0	?	?	0	?	?	?	?	2	?	?	?	?
Poorly known																	
aurea	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
edwardsi	0	?	?	?	?	?	?	0	0	0	0	0	0	0	?	?	?
erubescens	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
flindersi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
golaia	0	0	0	0	0	?	?	0	0	0	0	0	2/3	0/1	0	0	
millegrana	0	0	0	1	1	?	?	?	?	?	?	?	?	?	0/1	?	?
pallida	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
paroa	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?
phoca	0	0	0	0	0	?	?	0	0	0	0	0	2	?	0	0	?
prea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
punctifera	0	0	0	0	0	?	0	?	0	0	0	0	2	0	0	0	?

Characters	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**
Taxa	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**
Poorly known																	
purcina	0	0	0	0	0	?	?	?	0	0	0	0	?	?	?	?	?
rubescens	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
sauvagei	0	0	0	0	0	?	?	?	0	0	0	0	2	?	0	0	1
sibogae (A)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
stellifera	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
ylva	0	?	?	?	?	?	?	0	0	0	0	0	?	?	0	0	?
New species																	
Sp. A	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
Sp. B	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
Sp. C	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
Sp. D	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
Sp. E	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
Sp. F	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
Sp. G	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
Other ingroups																	
punctuolata	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
caespitosus	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	1
bimaculata	0	0	0	1	0	0	0	0	1	0	0	0	2	0	0	0	1
filix	0	0	0	1	0	0	0	0	1	0	0	0	2	0	0	0	1
grandiflora	0	0	0	0	1	?	0	0	0	1	0	0	2	0	0	0	1
estrelyado	0	0	0	0	1	0	0	0	0	1	0	0	2	0	0	0	1
capensis	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	1
complanata	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	1
araneosa	0	1	0	0	0	0	0	0	1	0	0	1	2	0	0	0	1
aivica	0	0	0	1	1	0	0	0	0	0	0	0	2	0	1	0	1
fanabensis	0	0	0	1	1	?	0	0	0	0	0	0	2	0	1	0	1
argo	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	1	1
tomentosa	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1
pardus	0	0	0	0/1	0	?	0	0	0	0	1	0	2	0	0	0	1
arbutus	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
pulchra	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1

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TABLE OF CONTENTS

BENOÎT DAYRAT: A Monographic Revision of Basal Discodorid Sea Slugs (Mollusca: Gastropoda: Nudibranchia: Doridina) 1